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CONTENTS

No. 1, March, 1935

PAGE

Ammonium in the Nutrition of Higher Green Plants ..... *Jose H. Pardo* 1
The Premaxilla in the Primates ..... *M. F. Ashley-Montagu* 32
Experimental Studies on the Duration of Life. XIV. The Comparative Mortality of Certain Lower Organisms ..... *Raymond Pearl and John R. Miner* 60
Results in the Phylogeny of a Genus of Snails ..... *V. Franz* 80
New Biological Books:
Brief Notices 87

No. 2, June, 1935

Biological and Medical Research at the Bureau of Science, Manila .. *Paul F. Russell* 119
The First Mammals ..... *George G. Simpson* 154
The Premaxilla in the Primates (*Concluded*) ..... *M. F. Ashley-Montagu* 181
New Biological Books:
Experimental Evolution ..... *Thomas Park* 209
Brief Notices 212

No. 3, September, 1935

The Cellular Transmission of Substances, Especially Neurohumors .. *G. H. Parker* 251
Reduplication in Evolution ..... *William K. Gregory* 272
Significance of the Biotic Community in Ecological Studies .. *Walter P. Taylor* 291
Differential Reproduction in China ..... *Herbert D. Lamson* 308
The Electro-Dynamic Theory of Life ..... *H. S. Burr and F. S. C. Northrop* 322
The All-or-None Principle and the Nerve Effector System ..... *A. Rosenblueth* 334
New Biological Books:
Brief Notices 341

No. 4, December, 1935

Some Historical Aspects of the Recapitulation Idea ..... *A. W. Meyer* 379
Morphogenesis of the Shoulder Architecture. III. Amphibia .. *A. Brazier Howell* 397
Delayed Implantation and Discontinuous Development in the Mammals
G. W. D. Hamlett 432
Genetics and Homology ..... *Alan Boyden* 448
New Biological Books:
Brief Notices 452
The Cost of Biological Books in 1935 ..... *John R. Miner* 492
Index to Volume 10 495

VOL. 10, NO. 1 MARCH, 1935

THE QUARTERLY REVIEW of BIOLOGY

AMMONIUM IN THE NUTRITION OF HIGHER GREEN PLANTS

By JOSE H. PARDO

Botanical contribution from the Johns Hopkins University, No. 119

I. INTRODUCTION

POSSIBLE sources of nitrogen for the metabolism of higher plants are nitrates, nitrites, ammonium compounds and a great variety of organic nitrogen compounds, such as amino acids and amides. Some of these are commonly taken up from the soil solution, like water and the salts that do not supply nitrogen, while some are usually not absorbed as such but are formed within the plant from simpler compounds previously absorbed. It has been suggested (85) that some seed plants, such as wheat, may actually assimilate small amounts of molecular nitrogen but most physiologists and agricultural chemists consider nitrification as probably confined to lower forms such as the nitrifying bacteria of the soil and the nodule-forming symbionts.

Although there is some evidence (99, 115, 154) that nitrites may be absorbed and assimilated by higher plants, yet it has not been shown that these compounds are commonly utilized directly, indeed they are usually omitted when nitrogen sources for higher plants are considered.

While there is no doubt that some ammonia (NH_3) may enter the plant through leaves or roots, from the surrounding air or from the soil, yet only a very small portion of the nitrogen required can generally be thus absorbed, and it is difficult to consider NH_3 as actually entering living cells, for it appears to react with water to give the NH_4 ion. Harvey states (54, p. 68), however, that this gas, applied through the leaves, is "much more toxic than it should be from the alkaline reaction it produces in the cell," resulting in "the overgrowth of tissues into hyperplasias if the concentration is very low." This observation raises questions that are clearly worthy of special study. Specific effects produced by foliar absorption of NH_3 may be related to some ions other than NH_4^+ itself, or to some other special conditions accompanying the presence of NH_4^+ when due to leaf absorption of NH_3 rather than to root absorption of ammonium salts.

Root absorption of amino acids and other organic nitrogen compounds has been reported (81) by some experimenters, and such compounds are probably ab-

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sorbed through leaves, haustoria, etc., in some special forms like insectivorous plants and parasites, but these compounds do not generally appear to be a significant external source of metabolic nitrogen for higher green plants. Salts of ammonium with organic acids should also be mentioned as possibly absorbed from the soil in some instances, but they seem to be of minor general importance.

It seems to be well established, however, that nitrate nitrogen is generally acceptable to all higher plants and that ammoniacal nitrogen is also acceptable under suitable conditions, at least, to many forms. Both of these sources of nitrogen are commonly present in the soil solution and in the waters of lakes and streams, but naturally their concentrations are usually relatively low. Nitrates are readily leached from soils and they are apt to be reduced to nitrites or even to ammonium salts through the action of microorganisms when conditions are suitable. On the other hand, ammonium salts, although they appear to be held in the soil to a greater extent than nitrates (68), are subject to alteration by soil bacteria, being thus oxidized to produce nitrites or nitrates. Soil bacteria may also transform a nitrite into a nitrate or into an ammonium salt, such as $(NH_4)_2CO_3$. Furthermore, the possibility that roots may sometimes exert an oxidizing or a reducing influence upon nitrogenous substances in the surrounding solution has not been excluded. It is therefore difficult to show clearly by simple experiments just what nitrogen compounds are actually absorbed by plant roots, even when it is possible to exclude nitrifying and denitrifying bacteria from some of the experimental cultures, and it is not easy to be sure that these bacteria have been excluded.

Nevertheless, experimental comparisons may be easily made with reference to the effects produced on growth and development by different nitrogen compounds when added to soils or sand cultures or when incorporated into culture solutions, and a great deal of experimentation has been devoted to such comparisons. From this kind of experimentation, taking account of the common possibilities of nitrification and denitrification, present agricultural theory with regard to nitrogen fertilizers has been developed.

Boussingault (18) seems to have been the first to show that nitrates are a very satisfactory source of metabolic nitrogen for many green flowering plants. He discovered the occurrence of nitrification in the soil, by which process ammonium salts and nitrites become oxidized to form nitrates; numerous investigators have subsequently studied nitrification in culture media. As soon as this process became appreciated most physiologists and soil chemists argued that the absorption and assimilation of ammonium salts was at least problematic, since these might be converted into nitrates, which, in turn, would be absorbed and assimilated.

Schattenmann's (138) field experiments with sulphate, chloride and phosphate of ammonium, which were referred to by Dumas (29), are interesting historically, as at least among the very earliest published evidences of the important rôle played by ammonia in bringing about the beneficial fertilizer effects obtained from the field use of stable manure. Of course these did not touch on the question whether ammonium salts are directly assimilated or are first converted into some other nitrogen compound, but they showed that the application of these salts to the soil led to markedly improved growth and larger crops in many instances. Schattenmann noted that alfalfa and clover failed to respond to this fertilizer treat-

ment. Dumas stated that Schattenmann had discovered this "rôle de l'ammoniaque dans la végétation" before 1835, whereas Liebig's statement (84) on that topic appeared only in 1840, in which year Dumas himself had expressed the same ideas, derived in part from a personal letter received by him from Schattenmann in 1836.

By the end of the nineteenth century students of plant nutrition generally agreed that ordinary green plants (with roots in soil or solution and stems and leaves in air) derive practically all of their assimilated nitrogen from the soil, either from salts of nitric acid (the NO_3 ion) or from ammonium compounds (the NH_4 ion). In Ewart's English translation of Pfeffer's *Plant Physiology*, which appeared about the beginning of the present century and which may be taken as fairly representative of the status of plant physiological knowledge at that time, it is stated (116, vol. I, p. 392) that green plants growing on well aerated soils (i.e., soils with considerable water content, but not nearly saturated with water) usually prefer their nitrogen in the form of nitrates. Other more specific statements from the same publication are as follows:

> "Most Phanaerogamic plants grow best when supplied with nitrates, but ammonium salts are more suitable for others. . . ." (*ibid.*, p. 403). "In Phanaerogams ammonium salts are always assimilated when present, however abundant nitrates may be" (*ibid.*, p. 404). "Neither Phanaerogams nor Algae appear to have the power of forming nitrates from ammonium salts by oxidation. . . ." (*ibid.*, p. 405).

Preference of swamp rice, notably when young, for ammonium salts rather than nitrates is especially mentioned (*ibid.*, p. 404) and it is added that "this is probably often the case in plants which grow in swampy or badly aerated soil, where the process of nitrification takes place slowly or not at all." It is pointed out, further, that "under natural conditions Phanaerogams rarely absorb organic nitrogen compounds . . . ." although such substances as urea, glycocoll, asparagin, leucin, tyrosin, hippuric acid, etc., may be absorbed and utilized as sources of nitrogen by flowering plants as well as algae under some conditions.

II. RECENT TEXT-BOOKS, HANDBOOKS AND GENERAL DISCUSSIONS

Authors of text-books and handbooks that have appeared in the last three decades appear to be in general agreement on the point that nitrates are generally utilized by ordinary green plants, but the question whether ammoniacal nitrogen may be commonly or only occasionally utilized by such forms seems to have remained generally about as Pfeffer left it. This question is specially difficult on account of the possibility that an ammonium salt, in an experimental soil solution or in a liquid medium as well as in ordinary field soils, may undergo oxidation with the result that the ammonium ion may seem to be absorbed and assimilated by the plants of an experiment even if nitrogen assimilation may actually be wholly or partially dependent on the absorption of the nitrate ion. The difficulty is further augmented by the logical possibility that—in some kinds of experiments at least—the ammonium ion may perhaps be absorbed to a considerable extent without being actually assimilated.

Most text-book writers agree that, while nitrates are generally more suitable for the nitrogen nutrition of higher plants, yet ammonium salts, other than the nitrate, are also assimilable, at least by many forms. One gets this idea from the books of Barton-Wright (10), Benecke and Jost (12), Green (43), Harvey (54), James (65), Jost (66), Nathansohn (104), Peirce

(112), Russell (135), Thatcher (149) and Torrey (152). In the American edition of Palladin's *Plant Physiology* (107) it is stated that "nitrates act chiefly, if not exclusively, as the source of nitrogen for higher plants," but at the same time references are given to some experiments that seem to indicate the direct utilization of ammoniacal nitrogen by some of these plants. Other writers consider that nitrates and ammonium salts are about equally suitable for the nutrition of higher plants in general; for example, Euler (36), Kostychev (76), and Maximov (91). The last-named author says (91, p. 54) that "they cannot be considered a more inferior source of nitrogen for plants than the nitrates."

Some writers of text books appear to doubt the general assimilability of ammoniacal nitrogen by higher plants. Raber (133, p. 77) says that ammonium salts are "of doubtful value in the direct nutrition of plants." Nathansohn (104), Peirce (112) and Leclerc du Sablon (136) appear to regard the question of ammonium assimilation as of minor importance, since ammonium salts are apt to be oxidized to nitrates in the soil. From the purely practical or technological viewpoint this may be a satisfactory view (since any soil may be supposed to contain nitrifying organisms as long as their absence has not been actually shown, which might in many cases be difficult in the field), but there seems to be no reason to doubt that the ammonium ion from ammonium salts may sometimes be a very important source of nitrogen, especially when the supply of nitrates is too limited. Hall appears to be inconsistent when he writes, in two books published in the same year, that "the higher plants doubtless take in the nitrogen they require as ammonia" (46, p. 221), and that "if ammonium salts are to feed the plants, they must be nitrified" (47, p. 67).

Still other authors of books on plant physiology seem to avoid the question of the direct assimilation of the ammonium ion by limiting their statements to the question of its absorption. In this group are Clements (21), Detmer (27), Duggar (30), Honcamp (58), Lepeschkin (83), Lyon, Fippin and Buckman (89), and MacDougal (90). Still others, such as Atkins (7), Barnes (22), Darwin and Acton (25), Ganong (39), Kolkwitz (73) and Timiriazeff (151), appear to leave the question of ammoniacal absorption and assimilation out of account altogether.

That plant forms seem to differ with respect to their ability to absorb or to absorb and assimilate ammonium salts and with respect to their "preference" for ammoniacal or nitrate nitrogen, was clearly stated by Pfeffer, as mentioned above, and similar statements are found in the more recent books of Linsbauer and Linsbauer (86), Lyon, Fippin and Buckman (89), Haas and Hill (45), and Jost (66). On this topic Miller's very recent book states (100, p. 503) that "the evidence indicates that some plants grow equally well with both nitrates and ammonium salts and that others, although assimilating ammonium nitrogen in the absence of nitrates, seem to prefer nitrates." Some of these differences may perhaps be related to the so-called "physiological acidity" of some ammonium salts when added to soil in which plants are grown. Thus Kostychev (76, p. 116) observes that "ammonia is nearly as good a source of nitrogen for seed-plants as nitrates whenever the plants can tolerate the resultant acid soil reaction or when the soil constituents at once neutralize the acids that are formed." On the other hand, there seems to be no reason to suspect that absorption of nitrate nitrogen may ever produce harmful effects through lowering of the H-ion concentration of the medium. It is commonly supposed that

plants differ with respect to their tolerance towards soil acidity and that such differences may explain some of their differences with respect to apparent nitrogen preferences. Several writers mention that plants seem to tolerate higher concentrations of the NO_3 ion than of the NH_4 ion. This point is clearly indicated by Euler (36), Jost (66) and Maximov (91).

Czapek (23, p. 307 *et seq.*) gives an account of the status of this problem of nitrogen nutrition about 1924, with a number of references to original contributions.

A valuable brief general discussion of the problem of the assimilation of the NH_4 ion by ordinary plants is to be found in Hutchinson and Miller's paper (63), which is accompanied by a bibliography of contributions that appeared before 1909. In their conclusion we read: "Some plants grow equally well with ammonium salt or nitrate as source of nitrogen. Other plants, while assimilating ammoniacal nitrogen in the absence of nitrates, appear to prefer nitrates. It is less certain whether ammonium salts can ever produce better final results than nitrates although we have indications that this may be the case." A brief discussion concerning what kinds of nitrogen compounds may supply nitrogen to plants was recently presented by Allison (2), who wrote:

> "No doubt nitrate nitrogen is the best source of nitrogen for the majority of plants and, under conditions where nitrates are present in relatively high percentages or where the conditions for rapid nitrification are favorable, it is safe to say that most of the nitrogen assimilated is in this form." "Nitrites may also be utilized by higher plants where the concentrations are low but they are so rapidly oxidized to nitrates that they ordinarily occur only in traces in soils and there is little reason for believing that plants secure much of their nitrogen in this form." "The writer has merely taken for granted that under average field conditions nitrate nitrogen is probably the most important nitrogen source for crops, but has pointed out that other forms may also be utilized to a greater extent than has generally been supposed."

Another representative general statement about the relative nutritional values of NH_4 and NO_3 may be found in Hoagland's recent paper (55, p. 628). He says that the H-ion concentration of the medium is very important when NH_4 is the source of nitrogen," the rate of absorption of nitrogen increasing with increase of p_H." He also points out that ammonium salts are more apt to be injurious to plants than are nitrates, unless various non-nitrogen culture conditions—including temperature and illumination as well as H-ion concentration—are carefully adjusted. Although NH_4 may be quite suitable as nitrogen source under properly adjusted conditions, yet "there is, in general, a greater range of safety in the use of nitrate nitrogen for the majority of agricultural plants studied."

Pirschle (119) wrote that both NO_3 and NH_4 are generally assimilated by higher plants, but that NO_3 may be superior to NH_4, especially when the medium is poorly buffered. In the same paper Pirschle presents an interesting brief review of the manner in which theory has altered in the last three decades. That review may be summarized as follows. In the last century it was at first held, following Kühlmann and Liebig, that NH_4 was the only nitrogen source for higher plants. When NO_3 was supplied it was supposed to be reduced to NH_4 in the soil, before being absorbed by roots. Boussingault's practical experiments (18) led to the opposite idea and then NO_3 was considered as the only—or at least the best—nitrogen source for higher plants. Through the work of many investigators it is now generally thought that both NH_4 and NO_3 may be assimilated by higher plants, but it is pointed out that they do not operate alike.

Ammonium salts are said to be "physiologically acid," while nitrates are physiologically neutral or alkaline. This

distinction was first explained, following Ad. Mayer (93), by supposing that NH_4 is absorbed more rapidly than SO_4 (when $(NH_4)_2SO_4$ is supplied, for instance), thus increasing the concentration of SO_4 and of the hydrogen ion in the medium. The increasing acidity was regarded as acting toxically on many plant forms and consequently NH_4 appears to be a very poor source of nitrogen for such forms. On the other hand, when $NaNO_3$ is supplied it was supposed that NO_3 is absorbed more rapidly than Na, with consequent *decrease* in the hydrogen-ion concentration of the medium, but that decrease may be hindered or prevented by extrusion of anions from the roots. Prianischnikow (128) and others went on to show, however, that $(NH_4)_2SO_4$ may be as good as $NaNO_3$, or even better, if acidification by the use of the former is prevented. Thus theory tended to revert to the older view of Liebig, but with the important difference that Liebig thought of reduction of NO_3 to NH_4 as occurring in the medium before absorption, while Prianischnikow thought that the NO_3 absorbed is reduced to NH_4 within the plant, as the first step leading toward the formation of amino-acids. There is much reason for supposing that NH_4 is actually the main internal source of nitrogen in amino-acid formation and if that is true it seems to follow that an ammonium salt should be superior to nitrates as external source of nitrogen, for plants that cannot tolerate high hydrogen-ion concentration in the medium, if and when the effect of physiological acidity is counteracted.

Recent studies on agricultural soils have led to further development of the theory of the physiological acidity of ammonium salts. A review of this advance was presented by Pierre (118) and a brief summary thereof may be found in Russell's textbook (135, p. 228). Many students of this question regard it as probable that nitrification in the soil, rather than selective absorption by roots, is the cause of the soil acidification that results from the use of $(NH_4)_2SO_4$ as fertilizer. According to this view, the NH_4 is first absorbed by the soil, uniting with soil anions and releasing some of the exchangeable soil bases to form sulphates with the released SO_4. Then the resulting absorbed ammonium salts of the soil are oxidized by nitrifying organisms, to produce nitric and soil acids, which are in turn neutralized by further reaction with remaining soil bases. Thus NH_4 is first oxidized to NO_3, which is the actual nitrogen source that is absorbed by the plants, and the increasing acidity of the soil is due to soil acids that are set free by the process of nitrification. It needs to be pointed out that this theory has been developed for soil cultures, in which exchangeable soil bases and acids are available, and that it supposes the rate of nitrification of ammonium salts in a soil to be greater than the rate at which NH_4 may be absorbed directly by the plants growing in that soil. In solution cultures in which $(NH_4)_2SO_4$ is the source of nitrogen increased acidity of the medium may be due apparently to either nitrification or to differential absorption. The equation for nitrification may be: $(NH_4)_2SO_4 + O_2 \rightarrow$ (nitrification) $\rightarrow 2HNO_3 + H_2SO_4 + 2H_2O$. The medium would thus become more acid without reference to absorption by the plants. On the theory of differential absorption NH_4 would be absorbed by the roots, leaving an excess of SO_4 to produce increased acidity in the medium.

The theory concerning utilization of NH_4 and NO_3 by higher green plants has been still further complicated on account of the findings of recent experimenters who have dealt with the influence of the

hydrogen-ion concentration of the medium on the suitability of these nitrogen sources for higher plants. Pirschle has dealt with this phase of the problem in several contributions and Mevius (97) has given it special attention. The last-named author has published extensive bibliographies (97, 98). Some of these H-ion relations will receive mention in the following section of the present paper. All that can be said about them in a brief general summary is that modern experimentation on the relative suitability of NH_4 and NO_3 as nitrogen sources involves careful attention to the H-ion concentration of the medium. General agreement as to these relations has not yet been obtained; different kinds of plants appear to behave differently and many other non-nitrogen conditions are apparently important in determining whether NH_4 may equal or may even exceed NO_3 in suitability.

It is not the writer's purpose to attempt here a critical review of the theoretical aspect of this problem; no clear picture of its present status is possible without an appreciation of the numerous experimental results that have been reported. Since these are not generally satisfactorily comparable (doubtless largely because of the employment of many different plant forms and many experimental techniques), the writer was led to the preparation of a sort of annotated bibliography of them and a portion of that bibliography is presented below.

III. REPORTS ON EXPERIMENTS

The numerous research articles bearing on the question of NH_4 *versus* NO_3 in the nitrogen nutrition of higher green plants are widely scattered. The present article represents a portion of the results of an attempt to summarize this part of the physiological literature. Attention is here confined to evidence based on growth, development, configuration, general appearance and yield. The writer hopes to present subsequently a review of the literature on studies carried out from the standpoint of physiological chemistry, employing quantitative analyses of the plant material and referring to rates of absorption and to the process of assimilation itself. In many cases both of these points of view are considered in the same published contribution, but it seems advantageous to treat them separately.

Only solution-culture experiments (including sand cultures to which solutions are added) are generally considered in this review. Practical field tests of nitrogenous fertilizers, which have been carried out in great number by many workers, are not generally referred to, since such experiments inevitably involve a much larger group of unknown influences or conditions than need to be considered when physiological cultures are employed, with which much more satisfactory controls are possible. Soil cultures and field tests pertain to agriculture or ecology rather than to physiology. It needs repeated emphasis that the solutions of practical problems in agronomy and horticulture are to be sought through actual field tests, while the related scientific or theoretical problems of physiology may be approached directly only through experimental use of well-controlled solution cultures. What may be the best nitrogen fertilizers in field practice or in soil cultures, with various soils and climatic complexes and with various methods of cultivation and rotation, is a technological question, for the answering of which fundamental physiological theory is not so important as actual field experience.

In this review nitrates are generally taken as basis for comparison, in attempt-

ing to estimate, as well as possible, the efficiency of ammonium compounds. There appears to be no record of any unequivocal tests in which NO_3 was found to be very unsuitable for the nitrogen nutrition of any higher plant, although NO_3 has been equalled or surpassed in effectiveness by NH_4. Our problem, for each plant form, is whether NH_4 has been found to be inferior, equal or superior to NO_3. When the numerical data for comparable tests differ by not more than 10 per cent the results are considered as about equal.

Attention should be called to the fact that the term *ammonium salts* usually excludes the nitrate and *nitrates* excludes NH_4NO_3. The last-named salt is of course both an ammonium salt and a nitrate. It is in a class by itself and requires special attention as such.

The contributions cited are presented in an arrangement of subsections according to the kinds of plants considered, the primary grouping being by plant families, which are arranged in alphabetical order. For each plant form the contributions are generally mentioned in chronological order. Numerical indices in parenthesis refer to the appended bibliography.

The material here presented was assembled in connection with a series of solution-culture experiments carried out by the writer on NH_4 assimilation by sugar cane, and some of the indications of those experiments are included here in the proper place. In the preparation of the manuscript of this review the writer has had the benefit of much helpful advice and criticism from Professor Burton E. Livingston, of the Laboratory of Plant Physiology of the Johns Hopkins University, where much of this work was done.

BALSAMINACEAE

An early experiment by Pirschle (119), with sand cultures, showed that garden balsam (*Impatiens balsamina*) grew better when N was supplied as $Ca(NO_3)_2$ or KNO_3 than when $(NH_4)_2SO_4$ or NH_4Cl was the only nitrogen source.

BROMELIACEAE

Stewart, Thomas and Horner (147) made an extensive study of the nitrogen nutrition of pineapple (*Ananas sativa*) in Hawaii and concluded that "under field conditions the pineapple plant probably uses nitrogen in both the nitrate and ammonium forms." Their experiments showed better growth with NO_3 than with NH_4 when the N content of the nutrient solution was 160 mg. per liter, but yields from NO_3 and from NH_4 were about alike when the N content of the solution was only 40 mg. per liter. They noted that the "crown" (the top cut off from the familiar pineapple fruit) was preferable to "slips" or "suckers" in culture experiments.

CHENOPODIACEAE

Pitsch (123), using potted plants of sugar beet (*Beta vulgaris*) in sterilized soil, found that NO_3 was preferable to NH_4 with regard to root production but NH_4 sometimes gave higher sugar contents. Dikussar's experiments with sugar beet (28) gave highest weight yields with NO_3 when the nutrient medium had a p_H value of 5.5, but NH_4 gave better growth than was given by NO_3 when the medium was neutral.

Krüger's experiments (79) with mangel were inconclusive as to this plant's response to NO_3 and NH_4; in one test NH_4 gave greater root yield than was given by NO_3 but two other tests showed NO_3 to be superior. Krüger employed both sterilized and unsterilized media.

Strawberry Blite (*Chenopodium capitatum*) was found by Pirschle (121) to grow better with N supplied as NO_3 than when the nitrogen source was NH_4, for

several different H-ion concentrations of the medium.

COMMELINACEAE

Wandering Jew (*Tradescantia fluminensis*) was included in the experimentation of Mevius (97), whose data indicate that NO_3 was superior to NH_4 in the nitrogen nutrition of this plant. But $(NH_4)_2SO_4$ gave fair growth in some experiments. Pirschle (119, 120, 121) also found, for a series of different p_H values of the nutrient solution and with continuously flowing as well as with unrenewed solutions, that NO_3 gave better growth of *Tradescantia viridis* and *Zebrina pendula* than was given by NH_4. Later continuous-flow experiments by the same writer (122) showed that NH_4 was superior to NO_3 for *T. viridis*; the optimal yield was obtained with NH_4 and a p_H value of 7.0.

COMPOSITAE

Perotti (114) included sunflower (*Helianthus annuus*) in the experimental series by which he came to the somewhat broad conclusion that flowering plants were able to derive their needed nitrogen directly from $Ca(CN)_2$. In Pirschle's tests (120, 121) sunflower gave larger yields with NO_3 as nitrogen source than when N was supplied as NH_4, but NH_4 appeared to be superior to NO_3 when the medium had a p_H value of 6.0.

CRUCIFERAE

In one of Krüger's tests (79) mustard (*Sinapis*) grew as well with NH_4 as with NO_3, but another test showed NO_3 to be superior. In Pantanelli and Severini's experiments (108, 109) mustard grew better with N supplied as ammonium tartrate or NH_4NO_3 than when it was supplied as $NaNO_3$, but the latter was superior to NH_4Cl or $(NH_4)_2SO_4$. Pirschle (119, 121) found, with both continuously flowing and unrenewed solutions, that NO_3 was superior to NH_4 for mustard, with a range of p_H values from 3.0 to 9.0. Another experiment (122) showed these two sources of N to be of about the same effectiveness.

Pirschle's experiments (119, 120, 121) gave results with rape (*Brassica rapa*) similar to those first obtained by him with mustard. In another experiment, with continuously flowing solutions, the greatest yields were about alike for NO_3 and NH_4, but NH_4 was superior when the p_H value of the solution was 5.0. The two nitrogen sources were about alike for a p_H value of 6.0 and NO_3 was superior for p_H values of 4.0, 7.0, 8.0 and 9.0. When both NO_3 and NH_4 were supplied together (as NH_4NO_3) the optimal yields (with p_H value of 5.0, 6.0 or 7.0) surpassed the best yields obtained with NO_3 as the only source of N. This combination gave results like those obtained with NO_3, when the solution had a p_H value of 4.0 or 8.0, and it was inferior to NO_3 with a p_H value of 9.0. Pirschle obtained very good growth of rape in flowing solution cultures with urea as the only source of N.

CUCURBITACEAE

Perotti's (114) results with pumpkin (*Cucurbita pepo*) were better with NO_3 than with NH_4, and the same is true of Pirschle's (119, 120, 121) tests of this plant, for a wide range of H-ion concentrations of the medium. On the other hand, Tiedjens and Robbins (150) grew cucumber to excellent fruiting in sand cultures in which N was supplied only as $(NH_4)_2SO_4$, in a solution having a p_H value of 7.5. Number and quality of fruits, as well as general growth, were as good as in commercial greenhouse culture. The photograph shown by these authors (their figure 8) is remarkably striking. When the p_H value of the $(NH_4)_2SO_4$

solution used was 5.4 growth was slow and leaves were small and light green, but when the p_H value was afterwards changed to 7.5 the foliage became dark green and subsequent growth was rapid.

ERICACEAE

Addoms and Mounce (1) found that cranberry plants (*Vaccinium macrocarpon*) produced noticeably greater runner growth with $(NH_4)_2SO_4$ than with $Ca(NO_3)_2$.

EUPHORBIACEAE

Pirschle's (119, 121) experiments with castor bean (*Ricinus communis*), in continuous-flow as well as in unrenewed solution cultures, gave greater yields with NO_3 than with NH_4, for a wide range of p_H values, but with a p_H value of 5.0 NH_4 was superior to NO_3.

GRAMINEAE

Because of their great economic importance, several of the Gramineae have been extensively experimented upon and a large number of contributions by many writers are to receive brief attention in this section. The annotations are brought together in subsections, as follows: Barley, English rye grass, Maize, Millet, Oats, Rice, Rye, Sorghum, Sugar Cane, Wheat; and a final subsection presents an attempt to summarize the experimental results for this family.

Barley (Hordeum vulgare)

The literature on the nitrogen nutrition of barley appears to begin with a paper by Ville (159), published in 1875, in which he reported that this plant gave good growth when N was supplied as NH_4Cl, as well as when the source of N was an organic compound such as urea. Ville did not report on nitrates. Pitsch's extensive experiments (123) with several varieties of barley grown in pots of sterilized soil gave better growth with N supplied as $NaNO_3$ than when $(NH_4)_2SO_4$ was the source of N. Kossowitsch (74) grew this plant in sterilized sand and reached the conclusion that both NO_3 and NH_4 were assimilated when they were supplied together. Krüger (79) tested barley in pots with a mixture of soil and sand, sterilized as well as unsterilized, and obtained larger yields with NO_3 than with NH_4 in some experiments while other experiments showed these two sources of N to be about equally effective. Ehrenberg's experiments on barley (31) gave superior yields with NO_3 and he concluded, from an extensive study of the whole problem of nitrogen nutrition, that NO_3 was the only suitable source of N for higher plants in aerated soils, although NH_4 might be assimilated from wet, acid soils. The results of Aso and Bahadur (6) indicated that NO_3 and NH_4 were about equally suitable as sources of N for barley, and a similar conclusion may represent the results of sand-culture experiments by Pfeiffer, Hepner and Frank (117). The last-named writers reported even better yields from NH_4NO_3 than from either NO_3 or NH_4 alone. From Prianischnikow's results with sand cultures (125, 126) it appears that $(NH_4)_2SO_4$ gave poor growth of barley unless it was accompanied by $CaHPO_4$, in which case growth was about as good as when $Ca(NO_3)_2$, $NaNO_3$ or NH_4NO_3 was used with $CaHPO_4$. Prianischnikow's best growth of this plant occurred when $Ca(NO_3)_2$ and the phosphate were used together. Nehring (105) grew barley to maturity in unrenewed sand cultures with different H-ion concentrations, using several different compounds as nitrogen source. Judged by grain weight, optimal yields were obtained with $(NH_4)_2SO_4$ and with $Ca(NO_3)_2$, which were practically alike, while $NaNO_3$, urea, and the other

nitrogen compounds tested were suboptimal. With a p_H value of 5, $(NH_4)_2SO_4$ and $Ca(NO_3)_2$ were equally effective, but the nitrate led to better yields with p_H values of 6 and 7 while the NH_4 salt was superior when the p_H value was 8. The best yield for $NaNO_3$ was obtained with p_H value of 5 and the best for urea was obtained with p_H value of 7. In sand cultures of barley, without washing or renewal of the solution, Pirschle (120, 121) found NH_4 inferior to NO_3 for a wide range of initial p_H values of the solution, but these two sources of N were about equally effective when the sand was subjected to frequent washing and renewal of the solution and when the p_H value of the solution was 7.0, 8.0 or 9.0. When the p_H value was below 7.0, NO_3 was superior to NH_4, even with frequent washing and renewal of the solution.

Summarizing the results obtained with barley, no one appears to have recorded any experiments in which NH_4 was found to be definitely superior to NO_3 for the growth of barley, but NH_4 has apparently equalled NO_3 in effectiveness when the experimental conditions other than nitrogen supply were suitable. It seems that growth of barley might be retarded by relatively high acidity resulting indirectly from the use of ammonium salts in the nutrient medium and that NH_4 might not be a suitable source of N for this plant unless experimental conditions prevented the development of excessive H-ion concentration or antagonized the toxic effect of acidity in some way. Ammonium nitrate seems to have been a suitable source of N for barley in experiments in which that salt has been tested.

English rye grass (Lolium perenne)

Pirschle's tests (119) indicated that NO_3 was superior to NH_4 for the nitrogen nutrition of English rye grass.

Maize (Zea Mays)

Among the earliest experimenters on the ammonium nutrition of maize was Hampe (48, 49, 50, 51), who employed solution cultures. He found that this plant grew well with N supplied as NO_3 but concluded that NH_4 of inorganic salts was absorbed and assimilated if the harmful effects of the acidity resulting from its absorption were not allowed to become too pronounced. He found urea superior to uric acid and glycocoll as good as nitrates for his maize plants. Kühn (80) also reached the conclusion that maize could assimilate NH_4 in solution cultures. His plants grown with NO_3 as the only source of N failed to mature but those supplied only with ammonium phosphate or with $(NH_4)_2SO_4$ reached maturity. Wagner (161) reported that young maize plants did not thrive when N was supplied as ammonium phosphate. Ammonium carbonate gave poor growth but its injurious effect was much less pronounced when the culture solution was kept nearly saturated with CO_2. He thought that glycine and creatine were absorbed and assimilated by maize. The conclusion that NH_4 was assimilated by this plant was also reached by Muntz (101), but Mazé (94, 95) thought that nitrification had occurred in Muntz's cultures supplied with NH_4 as the only source of N. However, when Mazé repeated Muntz's experiments the results were similar to those reported by the latter. Mazé came to the conclusion that NH_4 was as good as NO_3 if the N concentration were kept relatively low. He also noted that maize in advanced stages of development grew more rapidly with NO_3 than with NH_4. Gerlach and Vögel (41) carried out what appear to have been very careful tests with sterilized-solution cultures of maize, obtaining just as good growth with NH_4 as with NO_3. Perotti (114) also agreed

that NH_4 was directly assimilable by this plant. Lehmann (82) found that young maize plants gave better growth with NH_4 than with NO_3 but as his plants became larger and older NO_3 was superior. Direct assimilation of NH_4 by maize was confirmed by Kalinkin (67). With sterilized-sand cultures Schulow (142, 143) obtained better growth of maize with NH_4NO_3 than with $Ca(NO_3)_2$, in the presence of KH_2PO_4, but his best results with the phosphate were secured with asparagin as source of N.—Rautenberg and Kühn (134) failed to obtain good growth of maize with NH_4 as the only source of N but NH_4NO_3 gave larger yields than were obtained with NO_3 alone. Graftiau (42) furnished additional evidence supporting the conclusion that NH_4 was directly assimilated by maize, without previous transformation. That different varieties of maize showed different relations to NO_3 and NH_4 was reported by Brigham (19); pop-corn appeared to prefer NO_3 to NH_4 but dent corn grew better with N supplied as NH_4. With *Bacillus subtilis* in the culture medium, urea, asparagin and alanine each gave some very good yields in Brigham's maize experiments. Prianischnikow (128) obtained better growth of maize with NH_4Cl (along with $CaCO_3$) than with $Ca(NO_3)_2$. In another paper (131) the same writer says that Dikussar had found, for maize as well as for sugar beet, that NH_4 was superior to NO_3 when the p_H value of the medium was 7.0, while NO_3 was superior when the p_H value was 5.5. Mevius (97), using solution cultures, gave special attention to the question of the "physiological acidity" of ammonium salts and the influence of $CaCO_3$, aeration, and other factors in counteracting it. In general, his largest yields of maize were obtained with NH_4NO_3, and NH_4 alone was superior to NO_3 alone only when low concentrations were employed. Loo (87, 88), using solution cultures, obtained greater maize yields with $NaNO_3$ than with NH_4Cl or $(NH_4)_2SO_4$. Ammonium nitrate and $(NH_4)_2HPO_4$ gave yields as good as $NaNO_3$ in some tests but other tests showed them to be inferior to $NaNO_3$. Allison's (2) solution cultures gave somewhat greater weight yields with $(NH_4)_2SO_4$ than with $NaNO_3$ but use of these two salts together gave greater yields than were obtained with $(NH_4)_2SO_4$ alone. Pirschle's (119, 120, 121, 122) solution cultures with unrenewed solutions showed NO_3 superior to NH_4 for maize. Four experiments with continuously flowing solutions showed superiority of NH_4 to NO_3 when the p_H value was 5.8. With p_H value of 5.0, 6.0, 7.0, or 7.1 yields with NO_3 and NH_4 were about alike and NO_3 was superior when the p_H value was below 5.0 or above 7.0. Similar results were obtained in an additional experiment with continuous flow of solution, but in this the optimal yields were obtained when both NO_3 and NH_4 were present, as NH_4NO_3. In the acid range of p_H values the last-named salt gave better growth than was given by the use of NO_3 alone. In Pirschle's most recent experiment (122) the similarity of NH_4 and NO_3 was extended far into the alkaline range of p_H values, as far as 8.0.

Summarizing the results of culture experiments on the nitrogen nutrition of maize, good growth has been obtained in many instances when NH_4 was the only source of N and NH_4 has been found superior to NO_3 in some cases. Ammonium seems to have given about as good growth as was obtained with NO_3 when the nutrient medium was not too acid and especially when the N content of the medium was realtively low. Different varieties and different stages of development of the plants appeared to show different relations to NO_3 and NH_4. Am-

monium nitrate, which supplies both NO_3 and NH_4 together, gave better growth than was given by either NO_3 or NH_4 alone.

Millet (Setaria)

Ehrenberg (32) reported that NO_3 was superior to NH_4 as source of N for sugar millet.

Oats (Avena sativa)

As early as 1859 Knop (71) published a report on soil-pot experiments concluding that $NaNO_3$ and NH_4NO_3 were equally beneficial to oats, but that urea, hippuric acid and some other organic nitrogen compounds were not suited to this plant. Birner and Lucanus (15) concluded that NO_3 could not be replaced by NH_4 for oats, and Bener (13, 14) also failed to obtain good growth of this plant with NH_4 as source of N. Pitsch (123) compared NO_3 with NH_4 in experiments with oats and found the nitrate to be decidedly superior. Clausen (20) obtained better growth of this plant with $(NH_4)_2SO_4$ than with $NaNO_3$ but he was inclined to attribute this result to characteristics of the soil used. Of Krüger's (79) three experiments with oats, one showed NH_4 and NO_3 to be equally effective, another showed NH_4 to be superior and a third showed NO_3 to be superior. As for barley, so also for oats, this writer considered NO_3 and NH_4 as about equally good. Ehrenberg (31) failed to obtain good growth of oats with NH_4. While Prianischnikow (124, 130) found NH_4 inferior to NO_3 for oats, the former was apparently assimilated to some extent under some conditions; nitrate gave the best growth. From his sterilized-solution cultures Schulow (143) concluded that both NH_4 and NO_3 were suitable for oats in early growth phases but that NO_3 was a better source of N when the plants were more advanced. Pfeiffer, Hepner and Frank (117) found NO_3 superior to NH_4 for this plant. In the sand-culture experiments of Pirschle (119, 121) optimal weight yields of oats were obtained with NO_3, whether or not the sand was frequently washed, with renewal of the solution. In one experiment NH_4 gave some yields about as good as were obtained with NO_3, but only with solutions having p_H values as high as 7.0, 8.0, or 9.0. The best yield was with NO_3 and a p_H value of 5.0. In Pirschle's solution cultures, with continuous flow as well as without renewal, oats grew best with NO_3 as source of N. In later experiments Pirschle (120, 122) obtained about as good growth with NH_4 as with NO_3 when the p_H value of the solution was 6.0.

Summarizing the results on oats, the effectiveness of NO_3 as N source appears to have been closely approached by NH_4 in only a few instances and no report has been found in which NH_4 is shown to have been superior to NO_3 for this plant. The effectiveness of NH_4 seems to have depended on the H-ion concentration of the medium, probably also on other features. Oats appears to be much like barley in this respect.

Rice (Oryza sativa)

Readers who are specially interested in rice will find Kondo and Isshiki's recent bibliography (72) a very valuable aid. The study of the nitrogen relations of this plant seems to have begun with Kellner (70), who published in 1884. From experiments with solution cultures they concluded that both NO_3 and NH_4 were assimilated by this plant, but NH_4 gave best results with young plants while older plants grew better with NO_3 as source of N. In general, their best results were obtained when both of these sources of N were supplied together, as NH_4NO_3.

Nagaoka (103) found NH_4 superior to NO_3, confirming a similar conclusion of Daikukara and T. Imasaki (24). Aso and Bahadur (6) agreed with Nagaoka and went so far as to regard $NaNO_3$ as unsuitable for rice. Pantanelli and Severini (108) found, in sterilized-solution cultures, that $NaNO_3$ gave better growth than was given by NH_4Cl, about as good growth as was given by NH_4NO_3 or $(NH_4)_2SO_4$, but optimal yields were obtained when they used $(NH_4)_3PO_4$ or NH_4MgPO_4 as source of N. Krauss (77, 78) concluded, from soil-pot and field tests, that ammoniacal nitrogen was specially suitable as nitrogen source for rice. Perciabosco and Rosso (115) found that rice was peculiarly sensitive to nitrite poisoning. Kelley (68, 69), working in Hawaii, wrote that $(NH_4)_2SO_4$ led to "considerable increases in yield of straw and grain of rice, while nitrate of soda was ineffective." Harrison (53) found that NO_3 was effective on rice paddies while ammonium gave good results. Trelease and Paulino (156), working at Los Baños, employed pots of solution-saturated soil and studied the salt nutrition of rice by the method of triangular diagrams, which had been introduced by Schreiner and Skinner (139, 140), Tottingham (153) and others. Best yields of straw and grain were obtained with $(NH_4)_2SO_4$ but NH_4NO_3 was nearly as effective as the sulphate. Sodium nitrate and $Ca(NO_3)_2$ gave much less satisfactory growth. Espino (33) employed solution cultures of young rice plants on a rotating table in the greenhouse of the Johns Hopkins University, at Baltimore, and used the triangular diagram in choosing sets of salt proportions that would represent a wide range of logical possibilities. His best growth was obtained with NH_4NO_3; when NO_3 was the only source of N growth was only fair; when the source of N was NH_4 alone the best sets of salt proportions gave dry yields nearly as large as were obtained with NH_4NO_3 but what was taken as "ammonium injury" to the foliage was then present. Willis and Carrero (163) also held that nitrates were less suitable than ammoniacal nitrogen for rice. Loo (87, 88) compared $(NH_4)_2SO_4$, $NaNO_3$, NH_4HPO_4 and NH_4NO_3, and took the H-ion concentration of his solutions into account. In one test $(NH_4)_2SO_4$ gave largest yields and the three remaining salts gave good yields that were about alike. In another test yields from all four salts were good and nearly alike. Very poor growth was obtained with NH_4HCO_3 as source of N. Bartholomew (9) obtained better rice yields with $(NH_4)_2SO_4$ and with some organic nitrogenous fertilizers than with $NaNO_3$. Palisoc (106) found, with solution cultures, that NH_4NO_3 was greatly superior to $(NH_4)_2SO_4$, while $NH_4H_2PO_4$ led to poor growth. Fukaki's (38) solution-culture experiments with rice showed $(NH_4)_2SO_4$ as better than $Ca(NO_3)_2$ for vegetative development, but these nitrogen sources were about equally effective for seed production and $Ca(NO_3)_2$ was somewhat more favorable for seed maturation. Espino and Estioko (35) found that NH_4 was superior to NO_3 for young rice plants, but they held that some NO_3 was essential to healthy foliage and concluded that both NO_3 and NH_4 were required in cultures of rice when young. Pirschle's (121) sand cultures of this plant, with frequent washing and renewal of the solution, gave optimal dry-weight yields when N was supplied as NH_4, but NO_3 was superior to NH_4 in his cultures without renewal of solution. With regard to H-ion concentration of the medium, NH_4 was superior to NO_3 when the p_H value of the solution was 6.8, 7.0 or 8.0, but NH_4 was inferior when the p_H

value was 3.0, or 4.0. Pirschle's experiments with continuous flow of solution (122) showed as good yields with NH_4 as with NO_3, but NH_4 was superior when the p_H value of the solution was 5.0, 6.0 or 7.0 and the yields were about alike when the solution had a p_H value of 8.0 or 9.0. The best yields of all were obtained when N was supplied as urea or when NH_4 and NO_3 were supplied together, either as separate salts or as NH_4NO_3.

Summarizing the experimental evidence for rice, it seems safe to conclude that this plant has generally grown better with NH_4 than with NO_3 as source of N, in cultures as well as in paddy-field experiments. But some cultures gave equally good results with either NH_4 or NO_3 and in some instances NO_3 appeared to be somewhat superior to NH_4. Rice appears to have shown less sensitiveness to "physiological acidity" than most of the other plants whose nitrogen nutrition has been experimented upon. There seems to be no doubt that this plant is able to assimilate both NO_3 and NH_4 and some writers think that both of these ions are essential to excellent growth and healthy foliage. Ammonium nitrate has given very good results with rice.

Rye (Secale cereale)

Pirschle's experiments (121) with rye showed this plant to be much like oats and barley, generally showing optimal yields with NO_3 as source of N, with similar relations to the H-ion concentration of the medium. The ammonium ion seems generally to have been unsuitable as the only source of N for this plant.

Sorghum (Holcus sorghum)

Pirschle's (121) solution cultures with unrenewed solutions showed NO_3 to be superior to NH_4 as source of N for sorghum. When the solutions were renewed continuously NH_4 gave the largest weight yields with p_H value of 5.0 or 6.0, but NO_3 gave largest yields with lower or with higher p_H values. The writer of the present review has recently carried out a series of solution-culture experiments on sorghum, in the greenhouse of the Johns Hopkins Laboratory of Plant Physiology. The results of these tests, which have not yet been published, show that best growth was obtained when N was supplied as $Ca(NO_3)_2$ but NH_4NO_3 gave nearly as good growth. Fair growth was obtained with $(NH_4)_2SO_4$ as the only source of N. It appears that these sorghum plants were able to assimilate some of their required N as NH_4 but that their preference was for NO_3.

Sugar Cane (Saccharum)

McGeorge's (96) sand-culture tests gave good growth of sugar cane with N supplied as NO_3 but not when NH_4 was the only source of N. Van den Honert (59) found that NH_4 gave poor growth of sugar cane and attributed this to a characteristic root injury, which appeared in his NH_4 cultures. He recalled that Miss G. Wilbrink had previously observed a similar root injury in cane plants that had been subjected to the influence of ammonium salts. In Pardo's (110) preliminary solution-culture tests $NaNO_3$ was a very effective source of N for sugar cane. Urea gave fair results but cultures with $(NH_4)_2CO_3$, with certain amino acids or with guanidine as source of N showed very poor growth. Additional experiments by the same writer (111) indicated that $(NH_4)_2SO_4$, NH_4NO_3 and urea were decidedly inferior to $Ca(NO_3)_2$ for young cane plants but that older plants (after 20 or 32 weeks of solution culture) grew better with NH_4NO_3 than with $Ca(NO_3)_2$ as source of N. Considerable experimen-

tal evidence favors the tentative conclusion that sugar cane prefers NO_3 in its earlier phases of development but that NH_4 may be superior to NO_3 when the plants are more advanced.

Wheat (Triticum sativum)

Mayer (92), who published in 1874, thought that wheat might assimilate NH_4HCO_3 when absorbed through the foliage. Ville (159) found, as with barley, that NH_4Cl and some organic nitrogen compounds gave good growth of wheat, but he did not include nitrates in his tests. Pitsch's (123) pot experiments with sterilized soil included winter and spring wheat as well as barley and oats and he obtained better growth of wheat with $NaNO_3$ than with $(NH_4)_2SO_4$, just as in the case of the other two cereals. However, some of his tests with winter wheat showed $(NH_4)_2SO_4$ to be nearly as effective as $NaNO_3$. Pfeiffer, Hepner and Frank (117) found $NaNO_3$ to give better growth of wheat in sand cultures than was given by either $(NH_4)_2SO_4$ or NH_4NO_3, the latter being somewhat the better of these two ammonium salts. Perotti (114) obtained good growth of wheat in soil cultures with NH_4NO_3 and with $Ca(CN)_2$. Hutchinson and Miller (63), who used sterilized-sand cultures as well as solution cultures, found that $NaNO_3$ gave much better growth of this plant than was given by $(NH_4)_2SO_4$ but that when the latter salt was applied with $CaCO_3$ it gave about as good growth as was given by $NaNO_3$. With sterilized solutions Pantanelli and Severini (108) found $NaNO_3$ to be a better source of N for wheat than either NH_4Cl or $(NH_4)_2SO_4$, but $(NH_4)_3PO_4$ or NH_4MgPO_4 led to yields several times as large as were obtained with $NaNO_3$. In sterilized-sand cultures these same authors (109) found that KNO_3 gave better results than were obtained with either $(NH_4)_3PO_4$ or NH_4MgPO_4. Several organic salts of NH_4 were also tried, as well as phosphates. These writers concluded that the injurious influence of NH_4 salts of strong acids might be avoided through the use of NH_4 salts of weak acids. Loo's (87, 88) solution cultures of this plant gave about as good growth with NH_4HPO_4 as with $NaNO_3$, perhaps because the phosphate did not give rise to such high H-ion concentration as is apt to result from the use of $(NH_4)_2SO_4$ or NH_4Cl. Pirschle (119, 121) included wheat in his sand-culture experiments, with and without frequent washing and renewal of the solution, and found NH_4 and NO_3 about equally good when the p_H value of the solution was 3.0, 7.0 or 9.0; when the p_H value was 6.0 or 8.0, however, NH_4 led to the better growth and when the p_H value was 4.0 or 5.0, NH_4 was inferior to NO_3. In solution cultures, with continuous flow as well as with unrenewed solutions, Pirschle obtained better growth of wheat with NO_3 than with NH_4. Further experiments (120, 122) gave nearly the same optimal yields with NH_4 and with NO_3 but NH_4 was somewhat superior for p_H values from 6.0 to 9.0, while NO_3 was somewhat superior when the p_H value of the solution was below 6.0.

Summarizing, for wheat, NH_4 appears to have been about as suitable as NO_3, or even superior to it under some conditions. It again appears that the H-ion concentration of the medium may directly or indirectly influence the relative effectiveness of these two sources of N.

Summary for Gramineae

It appears that all the Gramineae tested were capable of deriving at least a portion of their needed N from NH_4 as well as from NO_3, but that the use of NH_4 as the only source of N has sometimes appar-

ently resulted in secondary conditions that were more or less injurious to the plants, notably high H-ion concentration of the medium. Different plant forms appear to differ in regard to their capacity to thrive with NH_4 as the only source of N and different varieties of the same species, as well as different developmental phases of the same form, have shown marked differences in this regard. The total concentration of the nutrient solution used and the partial concentrations of its component compounds (including the source or sources of N) appear to have exerted influences, either through resultant high H-ion concentration or otherwise, upon the apparent effectiveness of NH_4 and NO_3 as sources of N. Frequency of renewal of nutrient solutions has also been influential, as should be expected, since the composition of a solution in cultures without adequate renewal is subject to more or less rapid alteration through differential absorption by the plants.

Definite conclusions as to the relative capacities or nitrogen preferences of these different plant forms are not yet permissible, but it may be said that rice has greatly surpassed the other Gramineae tested, with respect to its tolerance of such injurious or retarding influences as may have resulted from the employment of NH_4 as sole nitrogen source. Under the various conditions of the experiments that have been carried out, rice has generally seemed to prefer ammoniacal N to nitrate N but it has grown better with NH_4NO_3 than with NH_4 alone as source of N. Maize and wheat appear to have grown about as well with NH_4 as with NO_3, under suitable conditions, but different sets of experimental conditions seem to have swung the apparent nitrogen preference to one or the other of these two sources; sometimes one was somewhat superior and sometimes the other. Maize has given better growth with NH_4NO_3 than with either NH_4 or NO_3 alone. Sorghum appears to have preferred NO_3 to NH_4 although the latter gave fair growth in some tests and good growth resulted from the use of NH_4NO_3. Sugar cane seems to have preferred NO_3 to NH_4 in early phases of development, while NH_4 or NH_4 and NO_3 together (NH_4NO_3) were superior to NO_3 alone in more nearly mature phases. Barley, oats and rye have generally given poor growth when N was supplied only as NH_4, while NO_3 generally gave very good growth. In no case did either of these three plant forms show superiority of NH_4; they seem to have been more sensitive to acidity of the medium than were any of the other Gramineae for which experiments have been reported. Barley has given good growth with NH_4NO_3 as double source of N. The use of this double source led, in some tests, to better growth than was given by either NH_4 or NO_3 alone, for rice, maize and the more advanced phases of sugar cane.

HYDROCHARITACEAE

Pirschle's (121) tests appear to indicate that NO_3 was more favorable than NH_4 for the submerged aquatic, *Elodea canadensis*, excepting when the medium had p_H value of 5.0, when NH_4 was superior to NO_3.

LEGUMINOSEAE

It is well known that legumes are able to obtain most, if not all, of their nitrogen requirements through symbiosis with nodule-forming bacteria when these are present, but it is also true that nitrogen compounds may be absorbed from the soil by these plants. The relations of leguminous plants to nitrogen compounds in the medium about the roots are especially difficult to study, since not only the nitro-

gen bacteria of the soil but also the symbionts need to be excluded from experimental cultures, or else taken quantitatively into account. For convenience, the notes of this section will be presented in a series of subsections representing the several plant forms considered.

Bean (Phaseolus vulgaris, P. multiflorus)

As early as 1842 de Saussure (137) reported that bean plants in sterilized sand were able to obtain their needed N from NH_4NO_3. Rautenberg and Kühn (134) reached the same conclusion, finding that NH_4NO_3, in solution cultures, gave better growth than was obtained when NO_3 was the only source of N. The use of NH_4 as the only source of N gave poor growth, but it led to a somewhat greater yield of seed than was obtained when NH_4NO_3 was used. Griffiths (44), growing young bean plants in sterilized solutions, found that they throve with $(NH_4)_2SO_4$ as the only source of N. With cultures of bean in sterilized and in unsterilized soil, Pitsch (123) obtained generally better growth and earlier ripening of seed when N was supplied as NO_3 than when NH_4 was the only nitrogen source. Nodules were plentiful on the roots of the plants in unsterilized soil but were not present when the soil had been sterilized. Loo (87, 88) found, with solution cultures of this plant, that $NaNO_3$ was superior to NH_4NO_3, NH_4Cl and $(NH_4)_2SO_4$; but NH_4HPO_4 led to as good growth as was obtained with $NaNO_3$. In Pirschle's (119, 120, 121) solution cultures, both without renewal and with continuous flow, scarlet-runner bean (*Phaseolus multiflorus*) generally gave greater dry weights with NO_3 than with NH_4, but in one series of tests with continuous flow these two sources of N were about equally effective. Pirschle's scarlet-runner bean plants did not appear to be very sensitive to differences in H-ion concentration, but continuous-flow cultures gave greatest dry weights with $(NH_4)_2SO_4$ when the p_H value of the solution was 6.0, the weights being smaller when the p_H value was lower or higher.

Pea (Pisum sativum)

Ehrenberg (31) cites Hosäus (60, 61, 62) as having shown that pea throve as well when supplied with NH_4 as when furnished with NO_3 as its source of N. Mazé (94) found with sterilized-solution cultures that pea grew very well when supplied with N only in the ammoniacal form. In Kossowitsch's (74) sterilized-sand cultures this plant gave good growth with N supplied as either $Ca(NO_3)_2$ or $(NH_4)_2SO_4$. Prianischnikow (129) obtained good growth of pea in sand cultures with NH_4HCO_3 as nitrogen source, better than with NH_4Cl. Hutchinson and Miller (63, 64) studied the nitrogen nutrition of pea with special precautions to avoid nitrifying bacteria, reporting that $NaNO_3$ and $(NH_4)_2SO_4$ gave good and approximately equal dry weights; some amino compounds gave better yields than were obtained with $(NH_4)_2SO_4$. Zaleski and Tutorski (165) obtained better growth of pea seedlings with NO_3 than with an ammonium phosphate, but sodium aspartate led to as good development as was obtained with NO_3. Schulow (142) obtained better growth of pea with $Ca(NO_3)_2$ than with NH_4NO_3. As in the case of bean, Loo's (87, 88) experiments with pea showed $NaNO_3$ superior to $(NH_4)_2SO_4$, NH_4Cl or NH_4NO_3, but NH_4HPO_4 was as good as $NaNO_3$. In Pirschle's (119, 120, 121, 122) experiments, pea gave better growth with NO_3 than with NH_4, whether the nutrient medium was continuously renewed or remained unchanged, and for a wide range of p_H values.

Vetch (Vicia)

In Mazé's (94) sterilized-solution cultures he found, for vetch as well as for pea, that NH_4 and NO_3 both led to good growth, being about alike. Prianischnikow (126) found, in sand-culture experiments, that vetch grew about equally well with either $Ca(NO_3)_2$, $NaNO_3$ or NH_4NO_3, but failed when N was supplied as $(NH_4)_2SO_4$. As for bean and pea, so also for vetch, Loo's (87, 88) solution cultures gave better growth with $NaNO_3$ than with NH_4NO_3, NH_4Cl or $(NH_4)_2SO_4$. Pirschle's (119, 121) results for vetch were also like those for bean and pea, NO_3 being superior to NH_4 for a wide range of p_H values. Windsor bean (*Vicia faba*), however, gave as good growth with NH_4 as with NO_3, when the p_H value of the solution was 5.0 or 6.0.

Lupines (Lupinus luteus, L. angustifolius, L. albus)

Lehmann (82) reported experiments with yellow lupine grown in sterilized sand, in which $NaNO_3$ gave much better growth than was obtained with $(NH_4)_2SO_4$. The seed yield was greater, however, from the plants supplied with the ammonium salt, in which case symbiotic bacteria were probably present, supplying fixed nitrogen derived from the air. Prianischnikow's (129) results with lupine in sand cultures showed that $Ca(NO_3)_2$, $NaNO_3$ and NH_4NO_3 were highly and about equally effective but $(NH_4)_2SO_4$ failed to give even fair growth. Loo's (87, 88) solution cultures of lupine showed that NH_4NO_3 was effective as nitrogen source and about equal to $NaNO_3$. In solution cultures, with continuous flow as well as without solution renewal, Pirschle (119, 121) obtained optimal yields of yellow lupine with NO_3 but NH_4 was also effective and it equalled NO_3 when the p_H value of the solution was 3.2, 4.5, 7.1 or 8.4. In sand cultures of blue lupine, with frequent washing and renewal of the solutions, the same author found that NO_3 was superior to NH_4, with a p_H value of 4.5 or 8.4, but NH_4 was about as effective as NO_3 when the p_H value of the solution used was 3.2, 5.8, or 7.1. The very best yields were obtained with NO_3.

Clover (Trifolium)

Knop (71) reported that clover was able to thrive in pots of soil supplied with NH_4, while hippuric acid and urea affected the plants injuriously.

Alfalfa (Medicago sativa)

Pirschle's tests (119, 120, 121) with alfalfa gave better growth with NO_3 than with NH_4.

Soy-bean (Glycine hispida)

Shive (144) found that NH_4 salts were toxic to soy-bean in solution culture. Wolkoff (164) obtained better growth of soy-bean in solution cultures with $(NH_4)_2SO_4$ and $Ca(NO_3)_2$ applied together than when KNO_3 was applied with $Ca(NO_3)_2$. In Pirschle's (119, 121) sand-culture tests NO_3 gave better growth than was given by NH_4, but other experiments indicated that this plant might do equally well with NH_4 as source of N if the effects of "physiological acidity" were avoided, as by means of solution cultures with continuous flow. When acidification was prevented in solution cultures NH_4 proved superior to NO_3 if the p_H value of the solution was 6.0 or 8.0. Tiedjens and Robbins (150) grew soy-bean plants in sand cultures with N supplied as $(NH_4)_2SO_4$ or as NH_4OH and with a p_H value of 7.0–8.8. Both of these sources of N gave very good growth, being equal or superior to $Ca(NO_3)_2$, but the sulphate was surpassed by the hydroxide.

Sensitive Plant (Mimosa pudica)

Bouchardat (16) placed cuttings of sensitive plant in solutions for rooting and observed that those in solutions containing NH_4 failed to develop.

Summary for Leguminosae

It appears that leguminous plants have been generally found to be capable of absorbing and assimilating NH_4 as well as NO_3. Bean and lupine generally seem to have preferred NO_3 to NH_4 as source of N, when NH_4 was supplied as salts of strong acids. For pea, some experiments have shown NO_3 to be superior to NH_4 and other experiments indicated that these two ions were about equally effective. Soy-bean seems to have been more susceptible than bean, lupine or pea to the physiological acidity resulting from the presence of NH_4 salts of strong acids, but nevertheless this plant seems to have been better suited to NH_4 nutrition than either of the other forms just mentioned.

With the exception of soy-bean in some experiments, none of the legumes tested appears to have given as large yields with NH_4 (and any tested p_H values) as were obtained with NO_3 when the p_H value of the solution was optimal for growth with NO_3. These plants seem to have been generally shown to be more or less unsuited to NH_4 and when both NH_4 and NO_3 were supplied together growth was not better than with NO_3 alone.

LILIACEAE

Aso and Behadur (6) obtained much better growth of onion (*Allium cepa*) when N was supplied as $(NH_4)_2SO_4$ than when it was supplied as $NaNO_3$.

LINACEAE

In Pantanelli and Severini's (108) experiments flax (*Linum usitatissimum*) showed as good growth with NH_4Cl, $(NH_4)_2SO_4$ or NH_4NO_3 as was obtained when N was supplied as $NaNO_3$. Ammonium tartrate gave optimal yields and NH_4HPO_4 was inferior to each of the first three salts mentioned. Pirschle (121) obtained equally good growth of flax with NH_4 and with NO_3 when his nutrient solutions were not renewed, but with continuously flowing solutions and a p_H value of 6.0, NH_4 gave better growth than was given by NO_3. These two ions were equally good when the flowing solutions had a p_H value of 4.0, 8.0 or 9.0.

MALVACEAE

In experiments on cotton (*Gossypium*), Holley, Pickett and Dulin (57) found that KNO_3 gave larger dry-weight yields than were obtained when N was supplied only as $(NH_4)_2SO_4$. Tiedjens and Robbins (150), using sand cultures of cotton, compared $(NH_4)_2SO_4$ and NH_4OH with $Ca(NO_3)_2$, finding that NH_4 gave as good growth as was given by the nitrate. Ammonium hydroxide led to even more vigorous growth than was obtained with the sulphate and no ammonium toxicity was observed. Best growth occurred with NH_4 when the p_H value of the medium was about 7.5 or 8.0. The disagreement between these results and those reported by Holley, Pickett and Dulin may be due to differences in the H-ion concentration of the solutions used. Naftel (102) has recently stated that his solution cultures and sand cultures of cotton showed that NH_4 and NO_3 together gave better growth than was given by either NH_4 or NO_3 as sole source of N; fruiting was earlier and more fruits were borne when both NH_4 and NO_3 were supplied together. Friedmann (37) appears to have carried out culture experiments with cotton using continuously flowing solutions with various H-ion concentrations. He employed $(NH_4)_2SO_4$, NH_4OH and KNO_3. Results

were to be reported in a later paper, which has not been seen by the writer.

MUSACEAE

Espino and Viado (34) found, with solution cultures of abaca (*Musa textilis*), that $(NH_4)_2SO_4$ was "a far better source of nitrogen" than $NaNO_3$.

POLYGONACEAE

Buckwheat (*Fagopyrum esculentum*) was found by Lehmann (82) to prefer NO_3 to NH_4, but Ville (158) obtained good growth of this plant when N was supplied only as NH_4Cl or as organic compounds. Pirschle (120, 121) found NO_3 superior to NH_4 for a broad range of p_H values of the medium.

ROSACEAE

Davis's (26) experiments with two-year old apple trees (*Malus malus*) in pots of sand showed no significant fertilizer effects of either $(NH_4)_2SO_4$ or $Ca(CN)_2$, whether the solution used had been sterilized or not, but markedly improved growth followed the application of $NaNO_3$. Tiedjens and Robbins (150) experimented with year-old apple trees grown in sand cultures in which they had been allowed to suffer from nitrogen deficiency, which gave yellow leaves. One group was treated with nutrient solution in which N was supplied as $Ca(NO_3)_2$ alone and another group received N only in the form of $(NH_4)_2SO_4$. Both solutions had a p_H value of 5.4. The foliage of the NH_4 plants remained yellow but that of the NO_3 plants became green. But complete recovery of the NH_4 plants occurred when the p_H value of the solution used was 8.0. In the same paper these authors state that the foliage of peach seedlings in sand culture was yellow when N was supplied only as $(NH_4)_2SO_4$ with p_H value of 5.4, but the leaves became green subsequently, after the p_H value had been changed to 8.0.

SOLANACEAE

Potato (*Solanum tuberosum*) was the subject of early experiments by Bouchardat (17), who used boxes of soil. He failed to obtain increased yields with ammonium salts. Stohmann (148), who used solution cultures, reported better growth of potato when NH_4NO_3 and $Ca(NO_3)_2$ were applied together than when KNO_3 and $Ca(NO_3)_2$ were applied together. Krüger (79) concluded, from soil-sand cultures, that this plant preferred NH_4 to NO_3, as source of N. His conclusion may refer to yield of tubers only, for his total-weight data show NH_4 superior in one test and NO_3 superior in another test and his results differ with respect to the concentrations employed. It apparently made no difference whether the soil-sand mixture had been sterilized or not.

Tobacco (*Nicotiana tabacum*), in Lehmann's tests (82), was greatly benefited by $NaNO_3$ but $(NH_4)SO_4$ led to yields twice as large as were obtained with $NaNO_3$. On the other hand, Pirschle (119) found that NO_3 was superior to NH_4 for tobacco. Wagner (162) reported that the burning quality of tobacco leaves was improved by the use of $(NH_4)_2SO_4$ as fertilizer but de Vries (160) thought that the burning quality was not influenced by fertilizer treatment. Using sterilized-solution cultures of tobacco Beaumont and his co-workers (11) reached the conclusion that nitrates were more readily assimilated than any of the other nitrogen sources tested; urea gave less satisfactory results, and NH_4 gave still poorer growth. They thought the unsuitability of NH_4 for tobacco might be only partially due to physiological acidity, as considered by

Prianischnikow (130), or to H-ion concentration, as considered by Mevius (97).

Tomato (*Lycopersicon esculentum*) was included in the sand-culture experiments of Tiedjens and Robbins (150), who compared $(NH_4)_2SO_4$ and NH_4OH with $Ca(NO_3)_2$ and found that NH_4 gave as good growth as was given by NO_3. Ammonium hydroxide with p_H value of 7, 8 or 9 was especially satisfactory and no injurious effects due to NH_4 were observed. (See the photographs shown in figure 4 of the paper just cited.)

UMBELLIFERAE

According to Pfeiffer, Hepner and Frank (117), $NaNO_3$ was superior to NH_4NO_3 and the latter was superior to $(NH_4)_2SO_4$, for growth of carrot (*Daucus carota*).

IV. CONCLUSION

Although the review presented in this paper is not to be considered as complete, it is probably fairly representative of the technique and trend of investigation in this field. Many different forms of higher green plants have been studied by numerous experimenters. Experimental technique has been continually improved. Nevertheless, it is apparent that the results reported do not yet lead to satisfactory general conclusions. It appears that the NO_3 ion is a suitable source of nitrogen for higher green plants in general but many forms have been found to thrive with the NH_4 ion as sole nitrogen source. In some cases these two ions, when supplied separately, showed about the same degree of effectiveness; in some other cases NO_3 was superior to NH_4, although the latter was nutritionally effective to a considerable extent; in a few cases NH_4 was found to be definitely superior to NO_3; and a good many tests indicated that NH_4NO_3 (which supplies both NH_4 and NO_3) was equal or superior to either one of these two ions supplied separately. Not only have different kinds of plants been found to show marked differences in their capacity to thrive with NH_4 as the only source of nitrogen, but different experimenters have in many instances obtained very different results with the same kind of plant, and separate but similar tests of the same plant by the same investigator have led to discordant results in some instances. It seems clear that such disagreement must be related to experimental influences or conditions that have not as yet been adequately reckoned with. A number of conditions that may possibly be involved will readily suggest themselves.

Differences among different plant forms, with regard to their NH_4 and NO_3 relations, are very striking and disconcerting when one tries to summarize these relations for higher green plants in general. There seems to be no reason for doubting that species and varieties probably do differ greatly in this as well as in many other respects, but the plants studied cannot yet be classified according to their preferences in respect to nitrogen supply. The apparent differences indicated by the literature and reflected in this review are not to be taken as really very well established, however, since the many experiments dealt with are generally not truly comparable in any satisfactory sense. Relatively slight differences in experimental technique may possibly account for great differences in results, without the supposition that the various plant forms are really as different as they appear to be. It is of course essential that the plants used in any series of comparable tests should be as nearly alike as possible at the beginning for all tests and varieties and genetic strains, as well as species, need consideration if definite results are to be expected from comparative experiments. Furthermore, the preliminary treatment of

the plants used (as in seed germination, for example) needs to be standardized, lest different lots of plants of the same form may differ in physiological vigor. The developmental phase of the plants used appears to be of great importance; nutritional requirements for different developmental phases and different degrees of vigor may be very different for the same variety of plant. Germinating seeds, sprouting eyes (as of sugar cane or potato), young plants, older plants, mature plants, all of the same species and strain, may be expected to perform more or less differently when exposed to the same environmental complex. Since the plants of an experiment change as they become older the time factor is naturally a crucial variable; results obtained with a longer experiment period may be quite unlike those obtained with a shorter period, even if all experimental features excepting duration are closely similar in the two cases.

In many instances it is difficult or impossible to institute useful comparisons among the results obtained in several different experiments because of the employment of different criteria in judging growth and development. A great variety of plant criteria have been used by experimenters on plant nutrition and different criteria may indicate markedly different relations to nutritional conditions. Green weight, dry weight, height, transpiration, leaf area, color, branching, flowering, fruit production, tuber production, are examples. Grain production and straw production are often compared, as in agronomic studies on cereals. Quality of the product is sometimes considered as well as quantity, and this consideration introduces many special kinds of criteria. Earliness or promptness of flowering, fruiting, and other events in the life cycle are sometimes important considerations in nutrition experiments; thus, if two different nutrient solutions are compared, with all other environmental influences alike, both may give sensibly the same result at the end of a sufficiently long experiment period, but flowering or fruiting may occur much earlier with one solution than with the other. Comparisons of growth vigor in different regions of the plant body may bring out important nutritional relations; for example, NH_4 has been found, in some of the writer's experiments, to give less root growth of sugar cane than was shown when nitrogen was supplied only as NO_3, while NH_4 appeared to be superior for top growth. The ratio of tops to roots may be a useful criterion for comparing cultures with respect to growth in general; in some tests ammoniacal nitrogen led to much more vigorous tillering in sugar cane than was obtained with NO_3.

Various special plant criteria refer to diseased conditions of the plants; for example, Tottingham's (153) magnesium injury to wheat foliage, which has recently been studied by Trelease and Trelease (157), and Espino's (33) ammonium injury to rice leaves. When diseased conditions occur they should naturally be taken into account, along with weight values or whatever general criteria are employed.

However species and varieties and different developmental stages of the same form may differ, there is certainly no doubt that the kind and degree of the nutritional response shown by any given plant species or variety toward any specified substance or ion is influenced not only by the nature and concentration of the substance or ion specially considered but also by concentrations and relative proportions of many other molecules and ions that are concomitantly present and effective in the nutrient medium. Hydrogen-ion concentration has recently been studied a great deal in connection with nitrogen nutrition and

other non-nitrogenous ions have received attention from some experimenters.

We may consider H-ion concentration for a useful illustration of the complications that became obvious as soon as non-nitrogen conditions are taken into account. Suppose that two fairly comparable series of satisfactory solution cultures have been simultaneously carried out with suitable plants, the sole nitrogen source being NO_3 for one series and NH_4 for the other. Also suppose that each series has included a number of different but maintained p_H values of the solution, ranging from 4.0 to to 9.0. The results might show that the p_H value of the optimal solution of the NO_3 series is 6.0, with a growth index of 1.10, while the p_H value of the optimal solution of the NH_4 series might be 8.0, with a growth index of 1.00. This might lead to the conclusion that the plants used, under the general conditions of this hypothetical series of experiments, had apparently preferred NO_3 to NH_4 as source of nitrogen, for the greatest growth index is shown for NO_3; but it would be noted that the best solution with NH_4 led to almost as good growth as was given by the best solution with NO_3. Such a conclusion would be based on the more general optima, without reference to p_H value, but a quite different conclusion might be reached if comparisons were instituted in the other direction, each two solutions with the same H-ion concentration being compared. For example, with p_H value of 6.0 the hypothetical growth indices for NO_3 and NH_4 might be respectively 1.10 and 0.80; and with p_H value of 8.0 the corresponding indices might be 0.80 and 1.00 respectively. From the first comparison (with p_H value of 6.0) NO_3 would appear to have been preferred to NH_4, but the second comparison (with p_H value of 8.0) would lead to the opposite conclusion. A study of the complete double series might lead to the generalization that NO_3 appeared to have been superior to NH_4 with suitably acid solutions but that NH_4 appeared to have been superior to NO_3 with suitably alkaline solutions.

Different plant forms have been found to differ in their preferences for p_H value of the medium as well as for nitrogen source. The complex problem of optimal H-ion concentration for the health of higher plants is discussed by Mevius (98), Arrhenius (5) and others. Whether NO_3 or NH_4 may be superior or inferior seems to depend largely on suitable adjustment of the environmental conditions other than nitrogen supply, notably H-ion concentration. The employment of NH_4 salts of strong acids as source of nitrogen is apt to result in H-ion concentration too high for healthy development in many instances. The eventual nutritional effectiveness of NH_4 for any plant seems therefore to be related, in many instances, to the degree of tolerance exhibited by the plant toward such resultant "physiological acidity." Rice appears to have shown generally a high degree of acidity tolerance.

The hypothetical example discussed above may illustrate, as a general and fundamental principle, how important it it is to include a representative range of p_H values in experimentation on nitrogen sources, and the same general principle requires attention with regard to other influential conditions, not only the concentrations of the other effective non-nitrogenous ions (as Ca^{++}, $HPO_4^{=}$, etc.) but the total osmotic value of the medium, temperature and temperature fluctuation, light intensity, quality of light and light fluctuation, and so on. Even for an adequately specified kind of plant, in an adequately specified developmental phase, it would be impossible to state definitely that either the NO_3 ion or the NH_4 ion is

always preferable to the other ion, for apparent preference in such a case is clearly conditioned by non-nitrogen features of experimental environment. When field culture is considered the theoretical problem of nitrogen sources becomes vastly more complicated, because of the practical impossibility of even attempting to take all influential environmental features into account. It is consequently not surprising that the very extensive literature of field tests with various nitrogen fertilizers is characterized by even greater discrepancy (at least as far as theory is concerned) than is shown by the literature of physiological cultures with which this paper deals.

As to the other non-nitrogenous ions commonly present in experimental media, the partial concentrations of PO_4, Ca, Mg, etc., may be expected to influence not only H-ion concentration but also a plant's response to a given concentration of NH_4 or NO_3 when applied along with a specified H-ion concentration. Many different experimental solutions might be made up so as to have the same p_H value and the same partial concentration of NH_4, but they would hardly be expected to be alike in nutrient effectiveness unless their other components had been suitably adjusted. Since the solutions used in different experiments on nitrogen nutrition have been very various with respect to their non-nitrogen constituents (even when their H-ion concentrations have been taken adequately into account) it is easy to suggest possible explanations for apparently discrepant results on this ground alone.

It has been noted that for physiological experimentation (as different from agronomic or other technological studies) soil cultures are unsuitable because of the innumerable unknown variables involved, but sand cultures have been used with relatively satisfactory results by many students of the problem of nitrogen nutrition, since such cultures bring into account some of the simpler soil features without necessarily complicating the experimentation to a hopeless degree. However, solution cultures naturally furnish the least troublesome procedure for experimentation and for the logical analysis of experimental results. Data derived from sand cultures may be very difficult to compare with corresponding data derived from solution-culture experiments, as is to be seen at various places in the present review. Such comparisons have been made by Shive and W. H. Martin (145), Hoagland and J. C. Martin (56) and Bakke and Erdman (8).

Another important possible source of discrepancy in experimentation on nitrogen sources, as well as on other phases of the problem of salt nutrition, refers to alterations that may occur in nutrient solutions after the plants have been introduced. This suggests not only the comprehensive question of differential absorption and possible excretion by plant roots but also the question of the presence or absence of micro-organisms in the experimental cultures, especially nitrifying and denitrifying bacteria. Trelease and Livingston (155), Allison (3), Allison and Shive (4), Shive and Stahl (146), Pirschle (119, 120, 121, 122) and others have indicated that continuously flowing solutions may be employed to avoid a number of fluctuating variables that are commonly encountered in culture experiments in which solutions are renewed at intervals. Flowing solutions have been employed by several experimenters in the study of nitrogen relations. It does not appear, however, that really satisfactory experimental procedure has thus far been at all widely applied for the prevention or quantitative experimental control of the effects of micro-organisms in culture solutions.

While arrangements are readily feasible by which a solution flowing into a culture jar is surely quite free from micro-organisms, yet it is not so easy to guard against the presence of micro-organisms on the roots of the plants when an experiment is started. Before really satisfactory experimental data on this question of the relative effectiveness of NH_4 and NO_3 can be made available the possibility of both nitrification and denitrification, as well as other changes apt to occur in the medium during a culture period, will need to be guarded against.

When continuous renewal of solutions is not resorted to, the relations between volume of culture jar, size of plants, number of plants per jar, concentrations and salt proportions of solutions, frequency of renewal of solutions and other related features, all surely require to be taken into account quantitatively. Perhaps many of the disagreements and apparent discrepancies of the literature reviewed in this paper may be related to some of these imperfectly understood variables.

Aeration of culture media is another feature of salt-nutrition experimentation that deserves serious attention, not only with reference to oxygen supply but also with reference to CO_2 concentrations and perhaps to concentrations of other volatile substances that may emanate from the roots or arise in the solutions. This feature may be standardized through the use of suitable arrangements for continuous renewal of solutions (3, 4).

Turning to the physical environment of experimental cultures, temperature, light quality, light intensity and fluctuations of light and temperature, are among the unknown or inadequately specified influences to which may be related some of the present confusion concerning nitrogen sources for green plants. Diurnal periodicity of temperature or of light, or both, may well be of paramount importance. The season of the year at which an experiment is performed may perhaps be indirectly influential in determining what sort of results may be obtained when two different solutions are compared (40).

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THE PREMAXILLA IN THE PRIMATES

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1. INTRODUCTION

THE present study owes its origin to the endeavor to determine whether or not the alleged early obliteration of the facial division between the maxillary and premaxillary bones in man may be regarded, as Professor Wood Jones has repeatedly affirmed, as "a definite human specific character" (100).

This endeavor has led so far afield that it may truthfully be said that the answer to this question now constitutes the least important part of this study. For, as we shall see, whether the processes of development which result in the facial obliteration or obscuration of the premaxilla in man are peculiar to him alone, or not, is a matter of no very great consequence in view of the remarkable series of morphological facts brought to light in this study, such, for example, as the peculiar form and relations of the premaxilla which, in man, have for the most part been unknown, and the nature of the involution which this bone has in man undergone and is still in process of undergoing. It will be shown that in the Primates without exception the form of the premaxilla is entirely dependent upon the functions it subserves, and that its form varies exactly in proportion as its functions vary. Finally, as a result of our observations certain biologic principles, seldom so clearly illustrated, will receive yet another demonstration of their validity. But this is to anticipate.

Ever since the publication of Vesalius' immortal *De Humani Corporis Fabrica* in the year 1543, the premaxillary bone has formed the subject of much contention, some of it extraordinarily vituperative, and some of it characterised by a vigor of expression which was apparently inversely proportional to the writer's understanding of his subject. The alleged absence of the premaxilla upon the facial aspect of the human skull was for long regarded by the earlier writers as one of the facts most significantly demonstrative of man's wide separation from the sub-human Primates and the remainder of the Mammals, and indeed, this belief is not yet quite exhausted, for it is still to be found, in a somewhat modified form and based upon a vastly more substantial series of observations than was available to the earlier students of the subject, in the writings of Professor Wood Jones, (85), (93), (100). To the history, however, of this subject, which forms one of the most interesting chapters of comparative anatomy, we will advert in the succeeding section of this study.

According to the viewpoint examined in the present work it is held that in the Primates, with the exception of man, the premaxilla may be observed upon the facial aspect of the skull suturally quite distinctly separated from the maxilla in almost all sub-adult as well as in many adult individuals. In late foetal and post-natal man no trace of the separation of this bone from the maxilla upon the face is to be observed, although the palatine portion of the premaxilla may be distinctly observed in the majority of infant crania, and may be encountered in some 26.0 per cent of adult crania. The latter

division of the premaxilla has been adequately dealt with by numerous investigators, and will therefore not be treated of quantitatively in the following pages. All Mammals, with the exception of the bats and certain edentates, possess premaxillary bones (102), but man alone of all the Mammals, so it is claimed, shows no trace of this bone upon the facial aspect of the skull either at birth or ever afterwards. The assertion is not that man does not possess a premaxilla, the presence of which has long been known in foetal and post-natal man, but that its identity as a distinct element upon the face is lost so early in development (about the end of the third foetal month) that this premature annulment of its status as an independent element must be regarded as a human specific character, since in the Primates inferior to man, and the Mammals in general, this bone remains facially distinctly separate from the maxilla until the attainment of a relatively advanced age.

Wood Jones' View

This view of the matter may be considered as it is expressed by its original proponent, Professor Wood Jones, for his views in this connection constitute the text to which this paper may, among other things, rightly be regarded as forming the critical commentary. I hope I need not say that in citing Professor Wood Jones' statements in this connection I have not the slightest wish to be polemical. Professor Wood Jones has of late years raised a large variety of interesting questions bearing upon the evolution of man—these questions require a definite answer, and in this study I wish merely to make one such answer to at least one of the most interesting questions he has raised. In his latest work (100) Professor Wood Jones writes,

> . . . . a definite human specific character is determined by the early loss of the facial identity of this element [the premaxilla] of the upper jaw. The human distinctions in regard to the premaxilla have often been minimized by comparative anatomists owing to misconceptions concerning the actual conditions present in *Homo*. It is easy to understand how Galen, familiar with the anatomy of Monkeys, but a stranger to the details of human structure, assumed that in man, as in Monkeys, there were two separate bones in the skeleton of the face, bearing the incisor teeth, and marked off from the maxillary bones on the face, as well as on the palate, by suture lines such as are present in the Monkeys. When in 1543, Vesalius affirmed that this facial suture line did not exist in man, although the limits of the os incisivum were at times distinct enough on the palate, his statement was regarded merely as an indication that the human skulls he had examined had departed from the standard of Galen's day.
>
> Camper was probably the first to claim that the absence of the facial separation of this element was a distinctly human characteristic. Following him, Blumenbach, who named the bone in question the intermaxillary, recognized its human distinction, and Sir William Lawrence went further, and regarded the premaxillary element as altogether absent in man, and emphasized the fact that in this character man was separated from all other animals.
>
> After Lawrence's day the question of the premaxillary bone became largely a debate as to its presence or absence as an element in the human skeleton, and its peculiarities as to early fusion on the face were somewhat neglected. Vicq D'Azyr, Goethe, Nesbitt, Leuckart, and many others showed what Vesalius had already affirmed, that the bone was in reality present in man, but that it was not marked off from the maxilla by suture lines after the sixth month of foetal life. Hamy and others devoted considerable attention to the question of the premaxillary-maxillary suture on the palate, and Albrecht, Warinski, Gils, Menard, and many others have carried the work on the palatal portion, and its ossification to great lengths. Owing to the work of these investigators there is now agreement as to the facts that the premaxilla remains separate from the maxilla on the human palate until the fourth or fifth month of foetal life; that by the sixth month, as a rule, the suture between it and the maxilla is closed, that in prognathous skulls, and in cases of rickets and hydrocephalus the closure of the suture may be delayed, and that in abnormal cases traces of the suture may even be visible in adult skulls. All this is a universally recognized anatomical fact concerning the formation of the palate; it does not, however, affect

the question of the fate of the premaxilla on the facial aspect of the skull. Regarding this point there has been much erroneous teaching. Ten years ago I drew attention to the fact that "when the human embryo is no more than 19 mm. long—that is about ten times the diameter of an ordinary pin's head—the premaxilla is losing its identity in the cartilage of the maxilla, and when the embryo is another 5 mm. longer it has ceased to exist as a separate entity on the face. The process by which the facial portion of the premaxilla becomes lost as a separate element is a complicated one, and it involves far more than the mere loss of the superficial suture line, for the whole method of growth of this part of the face is involved. The human premaxilla is lost in, and becomes overgrown by, the facial portion of the maxilla, but it still shows its independence of the maxilla, not only upon the palate, but within the nasal chambers." These statements were made as a result of an examination with Professor Fawcett of his unmatched material of developing chondrocrania in 1914, and they were made as a direct refutation of the erroneous teaching that has been put forward concerning the actual state of affairs present in *Homo*. In 1892 the distinguished author of the Cartwright Lectures laid it down as an anatomical truth that the human premaxilla is sometimes partially, and sometimes, but more rarely, wholly, isolated from the maxilla on the face. It was also affirmed that the junction of the two elements was effected late in certain races, such as Australians, New Caledonians, and Greenlanders. . . . .

The anatomical fact of the early loss of identity of the human facial portion of the premaxilla is not to be denied. Nor must its importance be overlooked. This obliteration of the facial premaxilla is a distinguishing character of man as a species; it would be used by the systematist as a specific diagnostic feature of *Homo*.

Now we have seen in Chapter III that although rigid interpretations of the Biogenic Law are no longer possible, nevertheless, there is an order in the acquirement of ontogenetic characters, and specific characters, being mostly acquired characters, are determined late in ontogeny. We know that there are many factors that produce upsets in the sequence of ontogenetic development, but allowing for all these, it is impossible to avoid attaching importance to this fact of the merging of the facial portion of the premaxilla in the matrix of the maxilla in the human embryo at so early a period as the 24 mm. stage. The more importance must be attached to it since, as Zittel remarks, "It is an unimportant character" (94). Being an unimportant character there appears to be no reason for its early translation to this early stage on any grounds of expediency in development. It is its very unimportance that renders it probable that its early ontogenetic accomplishment is guarantee of its early phylogenetic acquirement, and since it is a human specific diagnostic character such a finding is of considerable interest.

Is the obliteration of the premaxillary suture peculiar to man?

There is much in all these statements that is true; they require, however, a detailed examination, for apart from Wood Jones' own observations an exhaustive study of the literature dealing with this subject reveals the fact that up to the present time the facial aspect of the premaxilla in the Primates has been given comparatively little attention by previous investigators, and that where this attention has been bestowed the number of cases examined has been extremely limited. Conclusions based upon the examination of an inadequate amount and variety of material must be regarded with the greatest caution. Wood Jones has further constantly maintained that since "The premaxilla is never marked off by suture lines from the maxilla on the face . . . how far up the sides of the narial aperture the premaxillary element extends is therefore unknown in *Homo*," (100); it will be necessary to inquire into this matter, as well as into Professor Wood Jones' statements relating to the form and articulations of the premaxilla common in New World and Old World Monkeys. An important task will be to determine the period of closure, or the stage of development at or during which, the premaxilla loses its independence by uniting with the maxilla upon the face in the various genera of subhuman Primates, the purpose being to discover whether there exists a trend of significance, with respect to the period of closure of the premaxillary suture in any of the Primates, which may in some way be connected with the early obliteration of the

same suture in pre-natal man. Finally, when these observations have been completed and the data recorded and analysed, the general aetiology of the differences observed, such as the late persistence of the premaxillary suture upon the facial aspect of the skull in some Primates and its early obliteration in others, will be discussed.

If it can be shown that there exists a very definite tendency for the premaxillary suture to undergo obliteration fairly early in the development of some groups of sub-human Primates, and that in such Primates certain conditions are to be found which are not present in other members of the Order, something will have been achieved which may help us to understand that the existing differences, real as they are, between man and certain Primates with respect to the loss of identity of the premaxilla, are, in fact, demonstrative of a close rather than of a distant relationship between man and such Primates.

In the succeeding section some space has been devoted to a consideration of the work of previous investigators relating to the subject of the premaxilla, from the earliest to the latest times. A number of highly important studies have been rescued from an obscurity as profound as it has been altogether unmerited, and by their means certain most germane facts brought to light.

The literature dealing with the premaxilla is vast, and whilst more than two hundred separate works have been read in the preparation of this study, such only as have had a direct or fairly direct bearing upon the comparative anatomy of the subject have been noticed here. The Bibliography appended to this study may be supplemented by those given in the works of Hamy (46), Frison (68), and Franz (115).

What may seem to some a disproportionate amount of space has been devoted to the writings of the earlier anatomists who had in any way concerned themselves with the premaxilla. This has been done in order to put an end to the reigning confusion which exists with respect to what a particular authority actually wrote in connection with the premaxilla. Also, it was thought that an historical conspectus of the subject, based upon the words of each authority, would help to establish more accurately than is at present the case, where honor is properly due for discoveries generally credited to those who neither made nor even showed acquaintance with them. In the majority of cases authorities are quoted from the original first edition of their work; in a few cases it has unfortunately been impossible to obtain the original edition of the work referred to, so that a later or translated edition has had to be relied upon,—such works are noted in the proper place.

For the opportunity to examine most of the rare works mentioned in this study, and for the loan of many of them, I am deeply indebted to the New York Academy of Medicine and its Librarians. To the Library of the American Museum of Natural History, New York, I am obliged for the loan of the volumes containing the papers by Vicq D'Azyr and Leidy which have been used in this study, and for the use of many of the Journals referred to. To Miss Helen Bayne, and to her assistant Mr. Hyman Gross of the Library of Bellevue Hospital Medical College, New York, I am greatly indebted for help in procuring the various loan volumes.

To Professors Wingate Todd and W. M. Krogman, of the Laboratory of Anatomy, Western Reserve University, Cleveland, my best thanks are due for reading this paper in manuscript and for drawing my attention to a number of studies which I had completely overlooked.

The material reported upon in this study consists of some 9947 post-natal Primate crania, ranging in age from birth to adult life; of these crania 5277 are sub-human and 4670 human. In addition some 16 human foetuses, both white and negro, have been examined. Skulls examined for other purposes and mentioned hereafter are not included in this total of 9963 specimens. The detailed description of this material will be found in the pages which follow.

To the following gentlemen grateful thanks are due for permission to examine the collections of crania in their charge, namely:

Professor Sir Arthur Keith, lately of the Hunterian Museum, The Royal College of Surgeons, London; Professor J. Thomson, Department of Anatomy, Oxford University; Professor E. S. Goodrich, Department of Zoology, Oxford University; Dr. L. H. D. Buxton, Anthropological Laboratory, Oxford University; Mr. W. P. Pycraft, lately of the Department of Zoology, The British Museum of Natural History, London; Professor Le Gros Clark, Department of Anatomy, St. Thomas' Hospital, London; Professor W. K. Gregory, Department of Human and Vertebrate Anatomy, Dr. Robert T. Hatt, Department of Mammalogy, and Dr. Harry L. Shapiro, Department of Physical Anthropology, all of the American Museum of Natural History, New York; Professor J. H. McGregor, Department of Zoology, Columbia University, New York; Professor T. Wingate Todd, Laboratory of Anatomy, Western Reserve University, Cleveland; Mr. Henry Field, Department of Physical Anthropology, The Field Museum, Chicago; Dr. Adolph H. Schultz, Laboratory of Physical Anthropology, Johns Hopkins University, Baltimore; the late Aldobrondini Mochi, and Dr. Lidio Cipriani, Museo Nazionale, Florence; Professor Beccaria, Department of Zoology, University of Florence; Professor Sergio Sergei, Department of Anthropology, University of Rome; and Professors Gestro and Vincioguerra of the Museo Civico, Genoa.

To Mr. Benjamin Freiband, Instructor in Anatomy at the College of Dentistry, New York University, thanks are due for the careful supervision of the cold water maceration of the human foetuses reported upon in this study, and for permission to examine five of his cleared specimens.

2. LITERATURE

Vesalius

The critical and controversial literature dealing with the premaxilla begins with the publication of Vesalius' *De Humani Corporis Fabrica* in the year 1543 (5). In this work Galen's anatomy is subjected to a careful examination and at almost every point is found wanting. Perhaps the severest criticism which Vesalius has to make is uttered in the section of Osteology dealing with the *Superior Maxilla*. It will be recalled that before the advent and appearance of Vesalius' great work, mediaeval anatomy was dominated almost entirely by the teaching of the second Century Greek, Claudius (as he has been mis-named) Galen, (A.D. 131–201), one of the very greatest and most creative of biologists of all time, as he has rightly been called (95). His writings were voluminous and encyclopaedic, touching upon every phase of medicine and its practice. For fourteen centuries the *Corpus* of the Galenic opera constituted the supreme authority to which European medicine paid religious tribute. As a descriptive anatomist Galen will always occupy a very high place, even though many of his descriptions were inaccurate, for Galen's acquaintance with the intimate structure of the human body was a fugitive one, being based for the most part upon the dissection of monkeys, dogs, and swine. Galen's osteology is clearly simian, so that when he describes premaxillary suture lines upon the facial aspect of the skull of man he is clearly projecting a condition of simian origin which he undoubtedly did not observe in the human skull. It is interesting to note in passing that Galen was actually not the first anatomist erroneously to describe the premaxillary suture upon the facial aspect of the human skull; the priority belongs to Rufus of Ephesus (A.D. 98–117) who, in his little work on anatomy, after giving an accurate description of the zygomaxillary suture, makes the observation that *duas alias quae cerni queant in malis*, two other sutures, scarcely visible, are present on both sides of the face (on either side of the narial aperture), here undoubtedly referring to the premaxillary sutures. (1). Vesalius, in his lengthy section on the *Superior Maxilla* notices the exomesognathic portion of the premaxillary suture upon the palate of man but absolutely denies the existence of premaxillary suture lines upon the facial

aspect of the human skull as described by Galen. His account of the form and structure of the maxilla is masterly, and his criticism of the Galenic description telling. The relevant passages are far too lengthy to transcribe here, but their forceful cogency leaves one very definitely with the impression of Menenius that "the most sovereign prescription in Galen is but empiricutic." (*Coriolanus*, Act II, Sc. II). Following the appearance of his great work Vesalius was immediately fallen upon and attacked for his treasonable conduct against the traditional teaching of Galen. Tyson 1699 (15) over one hundred and fifty years later gives a good account of the controversy which followed; it is here reproduced in his own words. Tyson commences by quoting Galen as saying that

One ought to know the Structure of all the Bones either in a Humane Body, or in an Ape's; 'tis best in both; and then to go to the Anatomy of the Muscles.

What *Galen* advised, no doubt he practised himself, and observed both. But *Andreas Vesalius* will not allow him this. For in his great and excellent Book *De Corporis Humani Fabrica*, he all along tells us, that *Galen* gives us rather the *Anatomy* of *Apes* than of a *Man:* And in his *Epistola ad Joachimum Roelants de Radice Chynae* (6), his chief Design is to prove, that *Galen* never dissected a *Humane Body:* and that he is often mistaken in the History of the Parts, as also in their Uses; and that his Reasonings are frequently unconclusive.

Upon the coming out of *Vesalius* his first Book, he was warmly opposed by *Jacobus Sylvius* a Physician at *Paris*, who had formerly been *Vesalius* his Master in *Anatomy;* in a treatise stiled *Depulsio Vesani Cuiusdam Calumniarum in Hippocratis & Galeni Rem Anatomicam* (7). This was answered not long after by *Renatus Henerus*, who published another Treatise, *viz. Adversus Jacobi Sylvii Depulsionum Anatomicarum Calumnias pro Andrea Vesalio Apologia.* Sylvius afterwards procures a Disciple of his to write against *Vesalius*, who puts out, but unsuccessfully, *Apologia pro Galeno contra Andream Vesalum Bruxellensim, Francisco Puteo Medico Vercellensi Authore.* A scholar of *Vesalius, Gabriel Cunaeus*, makes a reply to *Puteus* in his *Apologia Francisci Putei pro Galeno in Anatomie examen.* Upon *Vesalius* his leaving *Rome*, a Disciple of his, *Realdus Columbus*, grew very famous for *Anatomy*, but ungrateful to his Master, as *Vesalius* complains in his Book *De Radice Chynae*, and his *Examen Observationum Falloppii.* But *Gabriel Falloppius* was always kinder to him, and mentions him with the greatest Honour, and calls him *Divine;* tho' in several things he dissents from him, which occasioned *Vesalius* his putting out his *Observationum Falloppi Examen* (10).

Seven years before the appearance of Vesalius' work Sylvius, following the Galenic tradition, had stated that he had observed the premaxillary suture upon the facial aspect of the skull in many human adult skulls (4). When then Vesalius 'presumed' to question the validity of the same statements in Galen, Sylvius, upon whose head the cap fitted only too neatly, chose to consider the criticism as a personal affront put upon him by Vesalius. He therefore delivered himself in 1551 of an attack upon Vesalius (7) so vitriolic that it probably remains unique and unparalleled in the annals of scientific literature. Of Vesalius himself Sylvius is pleased to say, in no round terms, that he is a madman as well as a liar. Whilst of the premaxilla he is content to say that undoubtedly Vesalius is wrong in his description of it, that is, in denying the existence of the facial premaxillary suture lines in the skull of the human species, and even though they may no longer be present upon the face of contemporary man there can be no doubt that the sutures were present in the skull of man in Galen's day!

Such a statement may today strike us as somewhat ludicrous, but in fairness to Sylvius, it should be remembered that Mediaeval Dogma, assisted by the teaching of the Church, laid it down as a necessary truth that man had departed considerably from the standards both of virtue and structure which had originally characterized Adam and Eve. The rate of evolution was speeded up or slowed down at the convenience of the Church, and so long as their statements could not be interpreted as conflicting with the received Dogma lay thinkers were at perfect liberty

to juggle that rate howsoever they pleased. Sylvius, among others, did not fail to take advantage of that liberty to heap reproaches and contumely upon the head of one whose heresy was that he had dared to think for himself and challenge the superstitions and the idols of his erstwhile masters.

The subsequent history of the premaxilla may be followed largely through the works of the seventeenth, eighteenth, and nineteenth Century anatomists.

Columbus, Fallopius

In the sixteenth Century, immediately following Vesalius, Columbus 1559 (8) and Fallopius 1561 (9) accurately described the palatal component of the premaxillary suture, but neither of them had anything to say of its homology with the same suture in lower animals. Columbus notes that the suture *ad utrunque* is present on both sides, *caninum dentem terminatam*, and terminates at the canine teeth, *quae in pueris conspicua est*, that it is conspicuous in the young, *in adultis autem sic aboletur*, and that in the adult, on the other hand, it is obliterated, *ut nullum sui vestigium relinquat*, not a vestige of it remaining. Fallopius merely notes that the suture in question is a transverse slit near the incisive foramen, "Nam reperio hanc divisionem, vel rimam potius esse, quam suturam, cum os ab osse non separet, neque in exterioribus appareat, vel cum os cum osse non conjungat; quod suturarum munus est si sub articulo debent." ". . . . a division or fissure rather than a suture, since it does not separate one bone from the other, nor does it appear exteriorly, nor join two bones, which is the function of sutures." Similar views with respect to the nature of this suture have been independently expressed by Kölliker (53) in the nineteenth and by Fawcett (78) and Jarmer (81) in the twentieth Century.

Seventeenth century anatomists

In the seventeenth Century both Ingrassias 1603 (11) and Riolan 1610 (12) range themselves with Vesalius against Galen, though Spigel 1626 (13) and Eysson 1699 (14), who give a description of the incisive suture, make no mention of the premaxillary suture. Towards the close of the century Tyson 1699 (15) in describing his *Orang-Outang*, which in reality was a chimpanzee, the skeleton of which is still preserved in The British Museum of Natural History, London, writes that "The *suture* of the *Palate* in our *Pygmie* was just the same as in *Man*. In a *Monkey* I observed that *peculiar suture Riolan* mentions, but did not find it in the *Pygmie*, only in the *Palate* of the *Pygmie* I observed a Suture, not from the Dens Caninus, as was in the Monkey, but from the second of the Dentes Incisores."

Nesbitt, Albinus

In the eighteenth Century the first work of importance with respect to the premaxilla is Robert Nesbitt's 1736 (16) cursory description of the completely isolated premaxilla in a human foetus entering upon its fourth month. All attempts to secure a copy of Nesbitt's volume have met with failure, but according to Hamy (44) the premaxillary sutures could be distinctly seen in Nesbitt's specimen upon the facial aspect of the skull. It would appear then that it is to Nesbitt that the credit belongs for having given the first description of the completely isolated premaxilla in a human skull.

Immediately following Nesbitt, Albinus 1737 (17) described and figured the endofacial portion of the premaxillary suture which in his specimen, a young individual, extended as far as the ridge of the inferior nasal concha.

Blumenbach

Blumenbach in the thesis which he submitted for the degree of Doctor of Medicine in 1776 (19), a work which has often been said to have laid the foundations of

modern physical anthropology, makes the following statements concerning the premaxilla:

"peculiare illud os, cui dentes incisores insident, maximam attentionem meretur. Es nempe homo caret, cum omnibus simiis plurimisque aliis mammalibus datum sit. Dubitabum quidem num quoque oran utan eodem instructus esset; cum nec Tysoniana nec Daubentoniana cranii eus icones curate satis essent, ut suturae probe distingui possent, neque Anglus auctor praecise satis de eo loqueretur: soluit autem nodum EXC. FR. GABR. SULZER, qui CAMPERUM virum eiusmodi animalia incidisse, idemque os in iisdem reperisse benivole mihi scripsit." "That particular bone in which the incisors are lodged deserves particular attention. This man is without, although all the apes and most of the mammals possess it. I doubted whether the orang-utan was equipped with this bone, since in the figures of Tyson and Daubenton (18) the skulls were not drawn in such a way as to render the sutures distinguishable: nor did the English author speak precisely about it: but his Exc. Fr. Gabr. Sulzer has settled the point, for he kindly writes me word that Camper, a great authority, has dissected animals of this kind and found this bone in them."

It is clear then that in this his earliest reference to the subject Blumenbach denied the existence of the premaxillary bone in the human skull.

Camper

It is often stated that Camper considered the absence of suture lines, that is, premaxillary suture lines, upon the facial aspect of the human skull as a distinctly human characteristic indicative of man's wide separation from the other mammals. A careful examination of Camper's complete works, together with Goethe's correspondence with Camper upon the subject (27) has failed to reveal as much as a single word that could be interpreted so. The work usually referred to as containing this statement (20) was first published in December 1778 and was concerned with the anatomy of various orang-utans. The only reference to the premaxilla in this work is as follows (the quotation is from the collected edition of the shorter works published in German translation from the Latin in 1784): Camper writes,

dass Oberbackenbein in zwei zertheilt, so das von der Nasenhöhle bis zwischen dem Hunds—und Schneidezahn eine Nalt lauft, wie bei allen Affen, Hunden, Katzen, Löwen und allen wiederkauenden Thieren, obschon diese oben keine Schneidezähne haben. Dieser vordere Theil enthalt im Orang von beiden Seiten die zwei obern Schneidezahne so wie es *Galen* sehr deutlich aus den Affen beschrieben hat.

Diese Eigenschaft allein bestimmt dem Orang seinem Platz unter den vierfüsigen Thieren. Ich besitze in meiner Sammlung Köpfe von Negern, Hottentoten, Kalmucken, Molucken, Chinesen, und von einer grossen Anzahl neu—und ungeborner europaeischen Kinder, ohne jemals einen einzigen Beweis dieser Trennung darinn gesehen zu haben.

There is no statement here, nor is there in his correspondence with Goethe on the subject, to the effect that man is unique in the absence of a premaxillary suture and therefore unlike all other mammals. Camper merely states that he has never observed this suture in man, having previously said that its presence in the orang-utan determines the latter's place to be among the quadrupeds; all of which is very different from what has customarily been attributed to him as having stated. Goethe, however, always believed that Camper obstinately refused to believe in the existence of this suture and therefore never saw it, but this may or may not have been the reason for Camper's shortsightedness.

Vicq D'Azyr

In 1780 (21) Vicq D'Azyr published a short paper, a study of three Primates, in which, among other things, he gave a description of the premaxilla in man and for the first time pointed out its ***structural equivalence*** to the same bone in other mammals. This paper is of unique importance since its description of the premaxilla in man, limited though it is, is the first to have been made upon a comparative basis.

Vicq D'Azyr's identification of this structure in man with the premaxilla of lower mammals proves that it is to him and not to Goethe, who published his paper some six years later, that the credit for the 'discovery' belongs. It is quite possible that Goethe was acquainted with Vicq D'Azyr's study, but if he was, he makes no mention of it in his own paper. Vicq D'Azyr's remarks on the subject of the premaxilla are of such classical importance, and the figures that accompany them of such interest, that it has been considered desirable to reproduce them here in order to render them more generally accessible. Vicq D'Azyr writes:

L'existence de deux trous incisifs dans la fosse buccale du mandrill, n'a rien qui doive surprendre, on le trouve dans le fissipèdes, tels que le chien, le chat; dans le bisulques, tels que le bœuf & le mouton; dans le solipèdes, tel que le cheval. En portant plus loin ses recherches, on observe, même dans le squellette des oiseaux, que la pièce mobile de la mandibule supérieure, ayant deux ouvertures latérales, établit entre la cavité du nez & celle de la bouche, une communication très-utile sans doute, soit au sens d'odorat, soit à celui du goût, soit à tous les deux ensemble, puisque cette conformation se trouve dans plusieurs classes d'animaux; c'est dans les bisulques & dans les solipèdes que ces trous ont le plus d'étendue, il y a même un os à double branche, spécialment (*o*) (Planche II, fig. 1 & 2, AB.) destiné à les former, & à soutenir les dents incisives lorsque la mâchiore supérieure en est pourvue; cet os, dans le cheval (*p*), dans le bœuf & dans le mouton (*q*), s'articule avec les os du nez & avec l'os maxilliare antérieur; il porte dans l'ouvrage de M. Vitet, le nom d'*os maxillaire inférieur* (*r*) (r Tome 1, p. 53). Le lapin, & en général les quadrupèdes qui ont quatre dents incisives, dont deux sous isolées à chaque machiore, montrent une disposition analogue; le deux incisive de la mâchiore antérieure sont implantées dans un os particulier qui termine la face, & forme les deux trous incisifs (*s*); (s. *Voy. pl. III, fig. 1, A* les deux dents incisives supérieures du lapin. *B.* l'os qui les soutient. *CD* la suture courbe qui les unit avec l'os maxillaire antérieure); moins la face est prolongée, moins aussi ces ouvertures sont amples, dans le chat elles sont étroite, & dans les singes cynocéphales elles sont plus grande que dans ceux qui ont la face plus courtel l'homme étant de tous les animaux celui dans leque: cette région l'est les plus, les trous incisifs doivent se rétrécir en même proportion, leur ouverture osseuse, double du côté du nez, est simple du côté de la bouche (*t*); (t Quoique cette ouverture osseuse soit simple & unique du côte de la bouche, il n'en est pas moins vrai que les Anatomistes exacts y demonstrent deux conduits, ce qui établit sous ce point de vue, une grande analogie entre la structure de l'homme & celle des animaux); mais il est important de remarquer que l'os maxillaire supérieure de l'homme présente souvent, sur-tout dans les jeunes sujets, derrière les trous incisifs & le long de la branche montante, une fêlure qui sépare la portion sur laquelle les dents incisives sont appuyées, d'avec le reste de l'os (*u*): (u *Pl. III, fig. 4*, os maxillaire humaine d'un jeune sujet: *A* partie du trou incisif dans la bouche; *B* un fêlure dont il s'agit, qui s'étend le long de lab ranche montante. . . . . *Fig. 5*, même os, vu en-dessous, du côté de la voûte palatine; *A* la partie la plus élevée du trou incisif; *A B C* suite de la fêlure susdite, qui s'étend jusqu'à la seconde dent incisive.): on ne peut s'empêcher de voir un rapport singulier & inattendu entre la structure de la portion osseuse qui, dans plusieurs quadrupèdes, sert à soutenir le dents incisives, & celle qui, dans les enfans au moins, a les mêmes usages (*x*). (x Voy. Anatomie de M. Sabatier, *tome 1, p. 55*). Il en est au reste de cet os comme de tous ceux qui composent la tête, les traces de sa séparation s'effacent avec l'âge, je l'ai cependant recontré dans quelques adultes (*y*); (*Voy. pl. III, fig. 2, A* partie du trou incisif; *B C* la fêlure le long de la branche montante, dans l'os maxillaire supérieure d'un adulte. *Fig. 3*, le même os d'un adulte, vu du côté de la face palatine; *A* la partie la plus élevée du trou incisif, *B C* le prolongement de la fêlure du côte du nez & la branche montante.); l'Anatomie comparée nous apprend donc pourquoi cette fêlure existe, & elle nous montre aussi qu'elle est l'ouverture respectiv des trous incisifs dans les différentes classes d'animaux.

These statements together with his figures prove beyond a shadow of doubt that Vicq D'Azyr was already acquainted, as early as 1780, with the form of the premaxillary bone in man as well as with its morphological significance.

Goethe

Goethe in his study of 1786 (22) described the inferior portion of the endofacial premaxillary suture, which, in certain cases in man he observed, as others

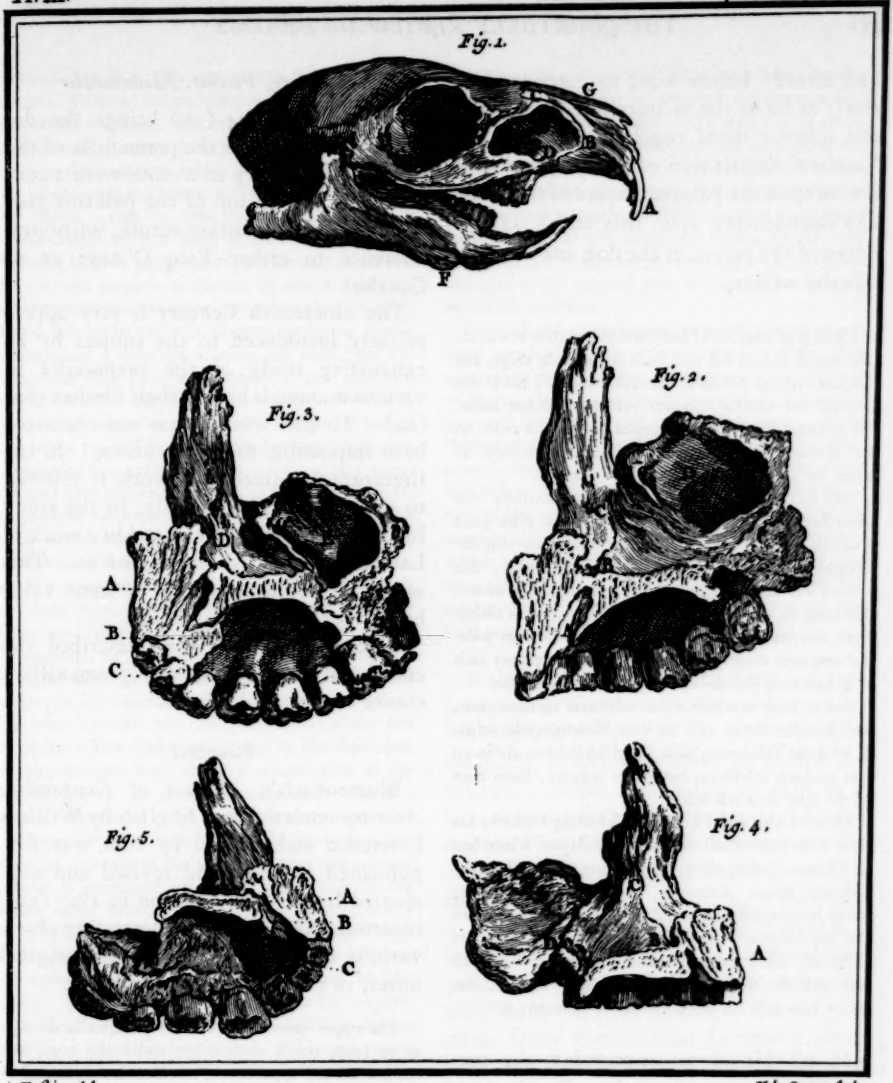

FIG. 1. THE FOLLOWING IS VICQ D'AZYR'S LEGEND ACCOMPANYING HIS PLATE III REFERRED TO IN HIS TEXT

Fig. 1. Skull of a rabbit. *A*. The two superior incisor teeth. *B*. The bone in which they are lodged. *C,D*. The suture which unites this bone with the neighboring bone. *G*. The nasal bone. *E*. The orbit. *F*. The mandible.

Fig. 2. Human maxilla of advanced age, viewed from the internal or medial aspect. *A*. Incisive foramen. *B,C*. The suture which extends along the ascending process of the maxilla. *D*. The maxillary sinus.

Fig. 3. The same bone viewed from the palatine aspect. *A*. Commencement of the incisive foramen. *B,C*. Line which shows the course of the suture; it extends up to the second incisor tooth of this bone. *E*. The maxillary sinus.

Fig. 4. The maxilla of a foetus, viewed from the internal or medial aspect. *A*. The incisive foramen. *B,C*. The suture which is prolonged upon the ascending maxillary process. *D*. Groove, called *palatine*, for the reception of the anterior border of the ascending process of the palate bone.

Fig. 5. The same bone, viewed from the palatine aspect. *A*. Entrance of the nasal foramen. *B,C*. Prolongation of the suture towards the alveolar border up to the second incisor tooth.

had already before him, to extend superiorly as far as the vicinity of the ridge for the inferior nasal concha. Referring to Vesalius' description of the premaxillary suture upon the palatine aspect of the skull and commenting upon this and Vesalius' figure of the suture in the dog and in man, Goethe writes,

> Denn jene erste Sutur hatte schon Vesalius bemerkt. Die zweite Sutur, die sich in Nasengrunde zeigt, aus den *Canalis naso-palatinus* herauskommt und bis in die Gegend der *Concha inferioris* verfolgt werden kann, hat er nicht bemerkt. Hingegen finden sich beide in der grossen Osteologie des Albinus bezeichnet: er nennt sie *suturas maxillae superiori proprias*.
>
> Am Sichtbarsten fallt des Os intermaxillare von Menschen bei n. 1 in die Augen. Man seht ganz deutlich die Sutur, die das Os intermaxillare von der Apophysi palatina maxillae superioris trennt. Sie kommt aus den *Canalis incisivus* heraus, deren untere Oeffnung in ein gemeinschaftliches Loch zusammenfliest, das den Namen des *Foraminis incisivi* oder *palatini anterioris* oder gustavivi führt, und verliert sich zwischen dem Hunds- und zweiten Schneidezahn.
>
> Bei n. 2 ist es schon etwas schwerer zu bemerken, wie dieselbe Sutur sich in dem Nasengrunde zeigt. Es ist diese Zeichnung nich die glücklichste; allein an dem meisten Schädeln, besonders jungern, kann man solche sehr deutlich sehen.
>
> Es wird also wohl kein Zweifel übrig bleiben, das diese Knochenabtheilung sich sowohl bei Menschen als Thieren findet, ob wir gleich nur einem Theil der Grënzen dieses Knochens an unsern Geschlechte genau bestimmen können, da die übrigen verwachsen und mit der obern aussern Theil der Gesichtsknochen nicht die mindeste Sutur oder Harmonie, wodurch man auf die Muthmassung kommen konnte, das dieser knochen bei dem Menschen getrennt sei.

In all his views concerning the premaxilla, it is evident that Goethe was saying essentially the things that Vicq D'Azyr had already said six years previously. In later years Goethe published a number of other papers on the premaxilla but these were concerned mainly with the consideration of the relationship of this bone to the varieties of cleft palate, and will therefore not be considered here.

Soemmering, Fischer, Rosenmueller

Soemmering 1794 (23) brings the descriptive anatomy of the premaxilla of the eighteenth Century to a close with a conventional description of the palatine portion of the premaxillary suture, without a reference to either Vicq D'Azyr or to Goethe.

The nineteenth Century is very appropriately introduced to the subject by an exhaustive study of the premaxilla in various mammals by Gotthelf Fischer 1800 (24). To this work it has unfortunately been impossible to obtain access. In the literature examined this work is referred to upon two occasions only, in the study by Goethe already quoted and in a work of Lawrence's soon to be referred to. This work, it would appear, is of some value but rather difficult to obtain.

Rosenmueller 1804 (25) described the endofacial portion of the premaxillary suture in two adult skulls.

Lawrence

Blumenbach's *Manual of Comparative Anatomy* rendered into English by William Lawrence and revised by him was first published in 1807, and revised and augmented by William Coulson in 1827 (26); it contains the following interesting observations on the premaxilla; the original notes, in parentheses, are included:

> The upper jaw-bones of other mammalia do not, as in man, touch each other under the nose, and contain all the upper teeth; but they are separated by a peculiar single or double *intermaxillary bone*, (Gott. Fischer *on the different forms of the intermaxillary bones in different animals*, with plates, Leipzig, 1800, 8vo; and Kool's *Annotationes Anatomicae*, Gronig. 1800, p. 5) which is in a manner locked between the former, and holds the incisor teeth. (*Vesalius De c. h. fabrica*, p. 46, fig. 1.) It exists also in the pecora, which have no incisor teeth in the upper jaw; as well as in such genera as have no incisor teeth at all, viz. the *duck-billed animal*, the *Cape ant-eater* and the proper *whales*. (On this account I prefer the term intermaxillary

bone to that of *os incisivum*, which is employed by Haller. Blair, in his excellent account of the anatomy of the elephant, calls it, *os palati*; and Vitet os maxillaire intérieur.) It is joined to the neighbouring bones by sutures, which run externally by the side of the nose and snout, and which pass, towards the palate, close to the foramina incisiva. (In human crania, at least those of the foetus and young children, there is at the same part a small transverse slit near the foramen incisivum, of which Fallopius gave the following accurate account in the year 1561: 'I find this to be rather a division or fissure than a suture, since it does not separate one bone from the other, nor does it appear exteriorly, nor join two bones, which is the office of sutures.' *Obs. Anat.* How far the alveolar portion of the superior maxillary bones marked by the fissure between them may be regarded as a rudiment of an intermaxillary bone, has been ably shown by Göthe, in the 1st vol. of his *Morphologie*. Compare Vicq D'Azyr *Mem. de l'Acad. des Sc.* 1780, and *Const. Nicati de Labii leporini congeniti Natura et Origine. Ultraj.* p. 25. In the celebrated dispute of the 16th Century, whether Galen's osteology was derived from the skeleton of man or the ape, Ingrassias argued from the latter side of the question, form Galen's having ascribed an intermaxillary bone to the human subject: and the same author, in his classical *Commentarii in Galeni Librum de Ossibus*, Panorm, 1603, fol. particularly points out the parts 'where Galen, led astray by the dissection of apes, deviates from the true construction of the human body.') Its form and magnitude vary surprisingly in several orders and genera of mammalia. It is small in many ferae, as also in the *walrus* (*trichechus*). In many of the *glires* (Its great size in these animals is accounted for by the magnitude of the incisor teeth which it contains) it is remarkably large, viz. in the *beaver* and *marmot*. It is also large in the *hippopotamus*, *porpoise*, and *cachalot*, (*Physeter macrocephalus*) and particularly projecting in the *wombat*. Its form is very remarkable in the *ornithorhynchus*, where it consists of two hook-like pieces, joined by a broad synchondrosis.† (†I cannot repeat here what I have observed in my book *De Generis Huma. Var. Nat.* on the subject of the intermaxillary bone; of which, as is there stated, not the least trace could be discovered in some *apes* and *baboons*, although the individuals were young. It must be inferred, that in these instances, it was consolidated to the neighbouring bones in their foetal state, when all the other sutures were nevertheless in a state of perfection.)

The want of the *os intermaxillare* has been regarded as a chief characteristic of the human subject; as one of the leading circumstances that distinguish man from other mammalia. That this bone is really wanting in man must be allowed, notwithstanding the doubts of Vicq D'Azyr. The well-known transverse slit, behind the alveoli of the incisors in the human foetus, would form a very slight and remote analogy between the human structure and that of animals; and when we consider that the superior or facial surface of the maxillary bones, so far from being marked by any suture, does not even bear a slit like that of the inferior part, it must be put entirely out of the question.

That all other mammalia possess this bone, is not quite so clear as that it is wanting in man. The exceptions occur in the quadrumana. In addition to those which the author has stated, it may be observed, that the head of an *orang-outang*, in the Hunterian Museum, which possesses all the other sutures, wants those which separate the intermaxillary bone. Tyson did not find this bone in his specimen of the animal, which was very young (see his *Anatomy of the Pigmy*), and it did not exist in a cranium which was delineated by Daubenton. I have also seen the crania of other monkeys, in which the sutures were all perfect and distinct, although this bone was wanting.

It should here be noted that the last two paragraphs above are the additions to Blumenbach's text by Lawrence. Blumenbach, it seems, is ready to accept the existence of the premaxilla in man as a fact, as is shown by his reference to Goethe and to Vicq D'Azyr. Lawrence, on the other hand, altogether refuses a premaxillary bone to man. His cursory reference to Vicq D'Azyr, and the words in which it is couched, indicate that Lawrence's acquaintance with the work he refers to must have been exceedingly slender. It seems fairly certain that Lawrence never saw Vicq D'Azyr's paper, for had he seen it he could hardly have dismissed it as easily as he does.

Meckel

The younger J. F. Meckel in his *Pathological Anatomy*, which was published between the years 1812–1818 writes, the quotation being from the English version of 1838 (28),

In several foetuses of three months, we have found it [the premaxilla] composed of three pieces; of these, the anterior comprises the portion of the palatine duct, with the nasal process; the middle, the body and the central part of the palatine process; finally, the third placed externally, the posterior part of this same process. The palatine canal, which is still only a simple hole, the *incisive*, or *anterior palatine foramen* (*foramen incisivum s. palatanium anterius*), appears enormous. The inner, the upper, and the posterior walls of the body are not yet formed. Then, *the anterior portion is separated from the posterior*, and a *real intermaxillary bone exists*,—a curious analogy with what is normally observed in almost all the animals inferior to man. Even when the two segments are not more entirely distinct, in the full-grown foetus and afterwards, the line of separation extends much farther, both in breadth and in length, across the palatine portion, so that it traverses all the breadth of the upper face. If oten happens that it does not stop there, but is reflected upward, and insulates a part from the internal face of the body as an internal thin layer, which is only applied against the external part. Further, a branch of this upper fissure goes inward, and passes behind the lachrymal channel, through the antrum Highmorianum to the posterior face of the body where it unites with the infraorbital canal. We also find some slight traces of this arrangement in the adult; it deserves to be remarked, as indicating, even in man, that the portion of the upper maxillary bone, in which the incisor teeth are situated, is separated from the others during the early periods of life, and then forms a real *intermaxillary bone* (*os incisivum intermaxillare*). We always find in the young foetus the internal branch of the fissure on the under face of the palatine portion, and this observation, together with the instances of division of the upper maxillary bone in the full grown foetus, seems to prove the primitive existence of a special piece of bone for each incisor tooth.

Leuckart

Leuckart's study 1840 (29) has not been available for examination, but according to Ranke (65) Leuckart described and figured the premaxillary bone in a human foetus of about twelve weeks in which the premaxillary suture was quite patent upon the right side of the face only.

Lawrence

Lawrence in his *Comparative Anatomy* 1844 (30) writes:

The want of the intermaxillary bone has been assigned by CAMPER as one of the grand characteristics which distinguish the human head from that of other animals.

The superior maxillary bones of the human subject are united to each other, and contain the whole of the upper series of teeth: they are, however, separated by a third bone of a wedge shape, which contains the incisor teeth, and was therefore called os incisivum. Since, however, this bone is found where there are no incisor teeth, as in the horned ruminants, in the elephant, and the two-horned rhinocerus of Africa, and also where there are no teeth at all, as in the ant-eater and some of the whale kind, BLUMENBACH* (*De Generis humani Varietate nativa, p. 35 [*sic* pp. 33–34] has bestowed upon it the more appropriate name of the os intermaxillare. It is a single bone in some cases: in many others, composed of two symmetrical portions. It is connected to the upper jaw-bone by a facial suture, running from the side of the nose to the alveolar margin, and by a palatine suture passing transversely from the alveoli to the anterior palatine foramina.

That man possesses nothing analogous to this intermaxillary bone of the brutes is so clear, that we cannot easily account for that excellent anatomist VICQ D'AZYR† (†Memoires de l'Acad. des Sciences de Paris, 1780) having discovered any analogy in the human jaw to the structure of quadrupeds. The only ground for such an opinion is the small transverse fissure in the palate behind the alveoli of the incisors, observable in the fetus and child, and sometimes tolerably distinct in the adult.† (†The fissure in question is more distinct in young than in old subjects, and it is called by Blumenbach sutura incisiva (*Beschreibung der Knochen.*) Although overlooked by several modern osteologists, it was observed and accurately described by the great anatomists of the sixteenth century, Vesalius, Fallopius, and Columbus. It is also mentioned by Riolan (*Anthropographia*, p. 649). Galen has expressly enumerated the intermaxillary bone among the component parts of the human face; and Vesalius very justly inferred from this, among many equally striking proofs, that the anatomical descriptions of that author, which had been universally received with the most implicit deference till that time, had not been drawn from the examination of the human subject. This attempt to rescue mankind from error and prejudice drew upon him nothing but hatred and reproaches from his contemporaries, who were driven to the most absurd arguments in defence of their idol Galen). But there is this very obvious and important distinction; that no vestige of a suture can even be traced in the human subject between the alveoli, much less on the upper and anterior surface

of the jaw: so that the similarity to the structure of the quadruped is very remote.

That all mammalia, besides the human subject, possess this bone is not so decidedly ascertained, as that man has it not, BLUMENBACH§ (§De Gen. Hum. Sect. 1, 15) found no trace of it in the crania of some simiae, although all the sutures were perfect; yet it is seen in the head of the orang-outang (*S. satyrus*) figured by him*, (*Abbildungen n.h. Gegenstände, No. 32) as well as in that of CAMPER.$ ($OEUVRES, pl. 1, fig. 3). On the contrary, in the head of a very anthropomorphous simia in the museum of the College of Surgeons, which seems to me to be the *S. satyrus*, not a vestige of the sutures separating this bone is to be seen, although the individual must have been very young, as the pieces of the occipital bone are not yet consolidated. According to TYSON and DAUBENTON it is not found in the chimpanse.

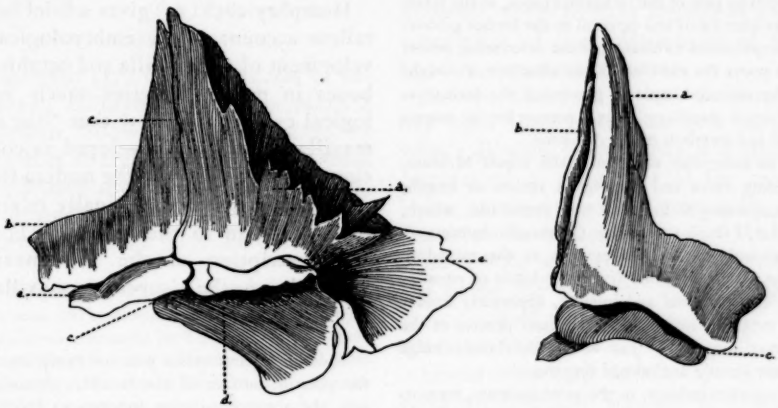

FIG. 2 A REPRESENTS THE SUPERIOR MAXILLARY AND INTERMAXILLARY BONES, MUCH MAGNIFIED, OF A HUMAN EMBRYO

The drawing was taken from the right side through the aid of the camera lucida, which reverses its position. *a*. superior maxillary bone; *b*. intermaxillary bone; *e*. alveolar groove.

FIG. 2 B REPRESENTS THE ANTERO-INFERIOR SURFACE OF THE SEPARATED INTERMAXILLARY BONE, MUCH MAGNIFIED

(From the left side but reversed by the camera.) *a*. ascending or nasal process; *b*. articulating surface for the superior maxillary bone; *c*. incisor alveoli.

Leidy

It is fitting that to Lawrence's strenuous belief in the non-existence of the human premaxilla the very next work to appear upon the subject should give the complete coup-de-grace. This work was a short paper by Leidy 1849 (31) in which a perfect description, supported by two figures, is given of the complete and independent premaxillary bone in man. The relevant part of this work together with the author's excellent figures are here reproduced. Leidy writes,

Recently having had an opportunity of examining several human embryos, in one of them I was fortunate enough to detect the intermaxillary bone as a distinct and independent piece. This embryo measured one inch and eleven lines from heel to vertex, and I presumed it to be about nine or ten weeks old. In it ossification had already advanced in the superior maxillary and intermaxillary bones sufficiently to give them a determinate form, and their appearance when magnified, is represented in the figures 1 and 2, [here figs. 2A and B], which were taken from the specimens through the aid of the camera lucida.

The greatest breadth of the two bones in apposition is one line and two-thirds; the greatest height, being at the ascending or nasal processes and part of the body of the bones; an alveolar ridge and groove and a palatine process projecting backward from the superior maxillary bone. They are easily separable at this period, and the articulation passes through the alveolar ridge, at a point corresponding to the separation between the incisor alveoli, and vertically upwards, dividing the nasal process into two nearly equal portions. On the posterior surface of the nasal process the articulation is at the bottom of a comparatively deep and wide groove, which, however, does not appear to be part of the lachrymal canal, as the latter appears afterwards and external to the former groove. The preparations exhibiting these interesting points which prove the existence of the same law, throughout the animal kingdom, governing the formation of the upper maxillary bones, I present for the inspection of the members of the Academy.

In an embryonic skeleton in the Wistar Museum, measuring three and one-eighth inches in length, and purporting to be about nine weeks old, which, however, I think too young, the maxillo-intermaxillary articulation is still evident at the ascending process, but it does not divide the latter so equally, being more internal and inferior, apparently from a more rapid development of the nasal process of the true maxillary bone. Just above the alveolar ridge they are already anchylosed together.

In another embryo, in the same museum, measuring three and one-fourth inches in length, the two bones have become firmly united, excepting behind the incisor alveoli, but the line of original separation is readily traced out, from a greater degree of thinness and transparency along its course. The nasal process of the true maxillary bone has so much increased beyond the nasal process of the intermaxillary bones, that the latter no longer ascends to the summit of the former, but is considerably inferior and internal.

In the foetal skeleton, measuring five inches in length, all traces of the inter-articulation have disappeared, except behind the incisor alveoli, which latter portion, as is well known, does not usually disappear until some time after birth, and in some instances is found in the adult cranium.

It is a fact worth noting that with the exception of Hamy (46) and Turner (55) Leidy's important contribution has been completely overlooked by all writers concerned with the subject since his day. Had Wood Jones, for example, been acquainted with this work, he could not have written as he has concerning our supposed ignorance of the form of this bone in man.

Pfeil, Lammers

Pfeil in 1849 (32) and Lammers in 1853 (33) each published a work on the premaxilla in man—which I have been unable to obtain for examination.

Humphry

Humphry 1858 (34) gives a brief but excellent account of the embryological development of the maxilla and neighboring bones in man, and cites much pathological evidence to show that "the intermaxillary bones are developed in connection with the vomer in the median frontal process and they are originally related to it rather than to the maxillary bones." His description of the 'intermaxillary portion' of the 'superior maxilla' is worded as follows,

A delicate linear suture may commonly be seen on the palatine surface of the maxilla, crossing from near the anterior palatine foramen to the interval between the lateral incisor and the canine teeth. This marks out the *intermaxillary bone*, which contains the sockets of the incisor teeth, constitutes the whole thickness of the alveolus, including the floor of the nostril, the anterior nasal spine, and the front wall of the superior palatine hole, and is connected above with the vomer and with the septal cartilage of the nose. The intermaxillary bones form a much more prominent feature in the lower animals. In them they are placed *in front* of the maxillae and are, therefore called "premaxillary bones," they also remain permanently separate from the maxillary bones, and send up a process to unite with the nasal bones on either side, so that, with the nasal bones, they complete the anterior opening of the nostrils.

Bryant, Rousseau

Bryant 1858/9 (35) gives the first description, of what was in later years to become an oft repeated observation, of necrosis of the premaxilla and the removal entire of this bone in a child of three years

following an attack of measles. A few years later 1864 (41) Bryant reported a case of exfoliation of the premaxilla in a laborer aged 40 years following a syphilitic infection acquired at the age of 17. This observation has also been repeated in numerous cases since.

Rousseau 1858/9 (36) attempted to prove, upon purely theoretical grounds, that the premaxillary bone was not normally present in man.

Salter

Salter 1860 (37) reports 20 cases of necrosis and exfoliation of the premaxilla in children following upon apparent recovery from an eruptive fever; two of these cases occurred after an attack of smallpox, four or five after measles, and the remainder after scarlet fever; he writes,

> The common characters of all the salient points of these cases and specimens lead me to conclude that the phenomena commence by damage done to certain of the teeth, and forming teeth during the eruptive stage of the fever; and that the bone necrosis and casting off of the teeth, temporary and permanent, and their containing alveoli and loculi is secondary and contingent upon such damage: that the *materies morbi* affects the teeth by virtue of their being members of the dermal or tegumentary system—the system upon which the poisons of the eruptive fevers spend their force, and that blighted and irretrievably destroyed, they light up in the surrounding periosteum an inflammation, which, while it is destructive, is curative—while it destroys the bone around—it effects thereby (as by that means alone it could effect) the casting off of the teeth as dead and effete organs.
>
> Such an interpretation is consistent with:
>
> (a). The fact that all these cases occur after, and are always associated with the eruptive fevers:
>
> (b). The age of the patient when they happen—from three to six years—a time when the most active nutritional changes are going on in the teeth, and (if the blood be poisoned), a time when the most poisoned blood would be circulating in these organs:
>
> (c). The symmetrical character of the disease. I have met with but one or two exceptions to this rule in about twenty cases:
>
> (d). The fact that the necrosis is limited to just so much bone, as will liberate the temporary teeth and the immature permanent, which are shed with it. To this limit I have met with but one exception, and that susceptible of explanation, from the exceptional circumstances attending the case: and
>
> (e). That it is unaccompanied by necrosis or exfoliation of any other bone of the skeleton.

Cleland, Jackson, Lewes

Cleland 1861 (38) in making a comparative study of the vomer, ethmoid and premaxillary bones in the mammals, seems, however, never to have arrived at a clear conception of the relationship of these bones to one another in man.

Jackson 1862 (39) reports the case of a boy aged three years and four months, who, following upon an attack of measles, complained of great pain in the mouth. Upon examination the premaxilla was found to be badly diseased. "A loose piece of bone was extracted, which turned out to be the right pre-maxillary bone, and contained the two incisor teeth. He did not attend again."

Lewes 1864 (40) in his *Life of Goethe* gives an excellent account of Goethe's discovery of the premaxillary bone in man, and acknowledges Vicq D'Azyr's right to the priority of the discovery. Lewes himself reports having seen a foetal skull in which the premaxilla was distinctly separated, and, he adds, "I possess a skull, the ossification of which is far advanced at the parietal sutures, yet internally faint traces of the intermaxillary are visible."

Vogt

Carl Vogt 1864 (42) in his admirable *Lectures On Man*, which has been available in the English translation only, makes the following remarks concerning the premaxillary bones,

> The incisors are inserted, in all mammals which have them, in a special bone, the intermaxillary, which is generally recognisable throughout life, and remains separated by sutures from those parts

of the maxillary bones which contain the canine teeth and the molars. The elements from which the intermaxillary is developed exist also in man, and are plainly perceptible in the foetus. But it soon becomes confluent with the other bones, so that even in the new-born infant the sutures are generally obliterated, and the union with the upper jaw complete.

At the beginning of this century, when the history of development had as yet made little progress, the absence of the intermaxillary was considered as a specific human character; and Goethe, assisted by that excellent anatomist, Loder of Jena, took great trouble to point out the error. At present it is only the early union which can be cited; but even this has its degrees. We sometimes find in young Negro skulls, as well as in skulls of idiots, traces of the maxillary suture; and, moreover, the sutures in apes are obliterated at various ages. Thus the sutures remain open in the gorilla to an advanced age, and are only closed in the oldest skulls, whilst in the chimpanzee the union takes place immediately after the change of the teeth. I have now before me skulls of the same age, of the genus *cebus*, in which the teeth had just been shed. In one genus (*Cebus apella*) the intermaxillary is plainly separated; in the other (*Cebus albifrons*) the union with maxillary is so perfect that there is no trace of any suture.

Smith

Smith 1866 (43) considered the relationship of the premaxilla to the varieties of cleft palate; in connection with these he writes" . . . . the perfect development of the true maxillaries, indicated by the invariable presence of the canines, is significant of the lesion [cleft palate] being one chiefly affecting or originating in the interposed structures; and in the more characteristic cases the disease is no doubt best marked in its effects on the intermaxillary bones." Double cleft palate, he points out, is generally due to complete absence of the premaxilla.

Eudes-Deslongchamps

Eudes-Deslongchamps 1866 (44) described the premaxillary suture in the skull of a five year old child from Balade. This description is referred to by Osborn in his Cartwright Lectures (64), and endowed by him with a significance which it apparently does not possess, for although it has not been possible to see Eudes-Deslongchamps' original paper, Hamy, fortunately, quotes it to the following effect: "The suture" writes Eudes-Deslongchamps "between the two bones divides the anterior palatine foramen, having attained towards its middle the canine alveolus. The suture is very clear on both sides. On the anterior inferior aspect of the face the suture is less evident and displays only a very narrow fissure which is hardly perceptible except by the use of a strong light." From this description it seems doubtful whether Eudes-Deslongchamps actually observed more than the palatine portion of the premaxillary suture.

Larcher, Hamy

Larcher 1868 (45) some ten years after the appearance of Rousseau's paper (36) already referred to, is at pains to cite the available evidence in order to refute the latter's statement to the effect that the premaxillary bone is not normally present in man. This he successfully does.

Hamy 1868 (46) in an excellent study of the premaxilla, considers the history, comparative anatomy, embryology, teratology, and pathology of this bone. He states that he has frequently observed the endofacial portion of the premaxillary suture in its entirety in human foetuses, some of which he figures. In a single skull of a New Caledonian infant he observed traces of the premaxillary suture on the right side of the face which were continuous with the palatine premaxillary suture between the canine and lateral incisor teeth. In the skull of a Chellouk infant he observed this suture to run to within a millimeter of the base of the nose. He states, further, that the premaxillary and facial sutures tend to remain open

much later in the prognathous negro races than in the orthognathous white races; this, he believes, is due to the fact that in the negro the facial portion of the skull continues to grow forwards over a period when the bones of the facial skeleton of the white have already attained their final form and relations.

Callender

Callender 1869 (47) was responsible for the first thoroughgoing *developmental* account of the premaxilla in man. Like another notable work with respect to the premaxilla, Callender's study has suffered almost complete oblivion. Its value will be appreciated from the excerpts. One of the main purposes of Callender's study was, in the words of the author, "to supply information regarding some few points with which we are as yet imperfectly acquainted, such as the growth of the maxillae, and the formation and eventual obliteration of the intermaxillary bones." Altogether, Callender examined 20 foetuses ranging between $\frac{1}{12}$ of an inch to 10 inches in length, or between 2 and 7 months of age. Describing a foetus of 2.3 inches, or about 10 weeks of age, Callender states that

> At the anterior extremity of the vomer the process of ossification extends to form the intermaxillary bones.
>
> These bones, though their appearances vary in different mammals, have amongst these animals certain common features. (1) The line of articulation with the superior maxilla is in front of the canine socket when the latter is present, when absent the relation of the suture to the maxilla virtually remains unaltered. (2) The premaxilla, as it is more correctly named for these animals, is prolonged superiorly to a point which ascends to a varying distance, or is cut short more abruptly. In any case, whatever be the length of the posterior margin, a groove is found in the anterior edge of the superior maxilla; and into this the wedge-shaped margin, broad or narrow (sometimes almost incisive, as in the sheep), of the praemaxilla is inserted, and is thus embraced, as it were, by the front border of the upper jaw. (3) The praemaxillae carry the incisor teeth, when present. (4) They articulate in the middle line, sometimes leaving a notch in front for a continuation forward of the septum. (5) They form more or less of the front of the palate, of the boundaries of the incisive foramina, and of the complete or partial septum which separates them.
>
> Passing to an examination of the human foetus, it is evident, from the shape and direction of the incisor process (which is best examined in a foetus 4.3, being then easily detached from the intermaxilla), that it passes across the anterior boundary of the nostril as the latter is continued forward to the middle of the lip. This boundary above is partly covered by the nasal process, below the palatal portion of the superior maxilla ends abruptly behind it, and between the two it is that the incisor process crosses, and indents the orifice of the nostril.
>
> The membrane inflected by the incisor process extends from the middle line (where it is continued forward to be connected with the process of the maxillary lobe which joins it on either side to complete the upper lip), partly below and then behind the incisor process, fills the fissure between that and the palatal, and is continued up behind the nasal process; the groove on the inner surface of this process corresponds with the edge formed by the bending in of the anterior membranous boundary of the nostril, and in the membrane continued back from the angle thus formed there is developed the plate of bone which constitutes the anterior inner or nasal wall of the antrum and the channel for the nasal duct, whilst in the membrane which lies anterior to the groove the intermaxilla of either side originates.
>
> In a foetus 2.3 [10 weeks] the intermaxilla consists of deposits of bone about the posterior edge of the incisor process, which subsequently grow down to form the plate of bone on the inner side of the middle incisor socket, and the posterior wall of the incisor sockets below and internal to the course of the incisor branches of the dental nerve. The front wall of the middle and lateral incisor sockets is continuous, as previously stated, with the plate of bone which covers in the canine notch.

Callender then describes and figures the premaxillary bone as a complete component of the superior maxilla in a foetus, 4.3, between 12 and 16 weeks of age. He concludes:

> The preceding observations account for the absence of all trace of the human intermaxillary bone on the facial aspect of the upper jaw in the adult, whilst the

permanent fissure through the palate and on the inner side of the nasal process are equally explained. The bone, in fact, is shut off from the face by the nasal and incisor processes of the superior maxilla. Distinctly outlined at the close of the fourth month; its nasal process, as it may conveniently be termed, is buried in that of the upper jaw, the apex assisting to form a permanent ridge for articulation with the inferior turbinate bone. In a foetus 1.5 I noticed a slight cleft in the nasal process of the superior maxilla corresponding with the top of the groove on its inner surface, but I have never seen anything like an approach to the formation of a distinct anterior plate of bone, such as forms part of the praemaxillae of mammals.

Yet despite the peculiarity which results from the formation of the incisor process and the shutting in of the intermaxillaries of man, these bones closely resemble those corresponding with them in mammalia. They have a similar wedge-shaped articular surface, fitting a groove in either superior maxilla; they extend towards the middle line and articulate there; they form the anterior extremity of the palate; they bound and divide the incisive foramina; they assist in forming no inconsiderable portion of the sockets for the incisor teeth; that they do not completely form them is a fact occasionally confirmed by the imperfect character of the sockets which lodge these teeth in those cases of cleft palate which have the intermaxillary bones isolated from the superior maxillae.

Another interesting point may be noticed. In some mammals having a slight upper jaw, a sheep for example, the outer wall of the nostril is smooth, there is no vertical ridge, such as that which in man rises to the turbinate bone. In other mammals with strong upper jaws the praemaxillae thicken towards their articulation with the superior maxillae, and here is the most prominent vertical line on the nasal surface; beyond this the superior maxillae recede somewhat. There is no such distinct ridge on the upper jaw itself. In man the corresponding ridge is placed about the middle of the ascending process of the upper maxilla, but it results from, and marks none the less, the junction of the nasal process of the intermaxilla with that groove on the inner surface of the upper jaw with which it originally articulated.

Callender's account of the development of the premaxilla in man has never been improved upon. Though numerous observers have concerned themselves with the same problem in the sixty-five years which have elapsed since the publication of his paper no one has observed so much and so well as he did. For example, the important fact that the premaxilla is replaced anteriorly below the pyriform aperture, entirely by the "incisor process" of the maxilla of each side, has been overlooked by all observers since his time, although Fawcett accepts Callender's description without, however, having confirmed it. It should be clear that as a contribution to the subject with which we are here dealing Callender's paper is of classic rank, since it provides, among other things, the first description and explanation of the changes in the facial skeleton which lead to the obliteration of the premaxillary suture upon the face in man.

Broca

Broca 1869 (48) in his splendid work on the Order of Primates gives a general summary of the existing knowledge concerning the premaxilla in some seven pages. He notices the early obliteration of the suture in the chimpanzee and the late persistence of the suture in the gorilla. Of the orang he writes "il résulte des observations que j'ai faites dans le musée du College des chirurgiens de Londres, qu'elle s'effectue après l'éruption des dernières dents de lait, vers l'époque ou sort la première molaire." In addition, Broca observes that in man the premaxillaries articulate with the nasal bones.

Sappey, Topinard, Holden

Sappey's *Anatomie* 1876 (49) provides a brief conventional description of the premaxilla in man, from which it is, however, impossible to gain an accurate idea of the complete form and relationships of this bone.

Topinard both in his short 1878 (50) and large 1885 (57) volumes on anthropology, has but a brief reference to the premaxilla.

Holden 1878 (51) in his *Osteology* gives

the usual ordinarily conventional description of the premaxilla.

Albrecht

Albrecht 1882 (52) in a study of the varieties of cleft palate and hare-lip is concerned to show that each half of the premaxilla develops from two distinct centres, each incisor tooth being supported by an individual premaxillary element, and upon this theory attempts to explain the various forms of cleft palate and hare-lip.

Kölliker

Kölliker 1882 (53) treated the heads of young embryos between 8 and 9 weeks of age with a 10 per cent solution of caustic potash. In from anything between an hour and 24 hours this solution rendered the soft parts of the head transparent, so that the white centres of ossification beneath were easily seen. According to Kölliker, the premaxilla is formed in the naso-frontal process at about the seventh week and unites with the maxilla at about the ninth. Each premaxilla contains two incisors; the enamel-germ, however, is formed as one continuous plate in the upper and lower jaws respectively, there is therefore no exact correspondence between the original formation of the bones and that of the teeth. It may thus be understood how in the case of double hare-lip the middle premaxilla contains sometimes two, and at other times three or four incisors, or even more.

Allen

Allen 1882 (54) gives a brief clear account of the premaxilla in the conventional manner. He believes that there are two centres of ossification for the premaxilla "one on either side of the median line in the position of the premaxillae of lower animals," and that these centres appear as early as the sixth or seventh week of development. Allen gives the following interesting description of a case of early loss of the premaxilla:

> A gentleman, aged sixty, was much annoyed by a defect which prevented his dentist fitting a plate for artificial teeth. The patient was edentulous, and had had from early childhood a cleft in the incisorial position of the upper jaw, which, as he had been informed by his parents, was caused by the loss of bone following an attack of measles. The cleft was a little to the right of the median line, and extended upward to the floor of the nose and backward along the roof of the mouth about an inch. The sides of the cleft were for some distance in contact, but posteriorly a delicate probe could be introduced into the nose. The entire right side of the dental arch was more incurved than the left. Acquired malformation of the hard palate, the result of early loss of the left premaxilla, was diagnosed.

Bland Sutton

Bland Sutton 1884 (56) describes the premaxilla in man as follows:

> It comprises that portion of the superior maxilla which lodges the two incisor teeth; from its mesial surface a horizontal portion projects backwards to form the inner boundary of the anterior palatine canal. Superiorly it has a vertical portion, which forms the lower and outer boundary of the anterior nares, and in well-marked cases it sends up a spiculum to articulate with the nasal bone.
>
> Dr. Paul Albrecht recently communicated to the Société d'Anthropologie de Bruxelles a paper to the effect that the premaxillary bone is, as a matter of fact developed from two centres, and supports his view by references to cases of cleft-palate and hare-lip. I have examined some cases of cleft-palate and can support Albrecht's statements, but in the normal condition there is only one centre for each premaxillary bone. The discrepancy may be thus explained: the premaxilla is originally developed in membrane, and at some little distance from the median line, which, in the foetus, is occupied by the thick cartilage known as the ethmo-vomerine plate. After a time the premaxillary ossifications involve the anterior extremity of the cartilage, so that the inner portions of these bones are really of cartilage origin. If anything interfere to prevent the premaxillary bone or bones meeting the ethmo-vomerine plate, the tip of this cartilage ossifies on its own account, and gives rise to the false notion of two centres occurring normally.

Bland Sutton has some good figures of the human premaxilla.

Turner, Broca, Berard

Turner 1884 (55) discusses the relationship of the form and structure of the premaxilla to cleft palate. Among seven infant skulls Turner found two in which the premaxillary suture was visible on the palate, on the floor of the nose, and on the nasal aspect of the ascending process of the superior maxilla.

Broca 1887 (58) similarly discusses the relationship between the premaxilla and cleft palate.

Berard 1888 (59) investigated the premaxilla in the Primates, but unfortunately I have been unable to obtain an idea of his results owing to my inability to obtain a copy of his work.

Kölliker, Biondi

Kölliker 1888 (60) sustains the view that the premaxilla is ossified from two distinct centres, one on each side of the median line.

Biondi 1888 (61) in an accompanying discussion disagrees with Kölliker concerning the number of ossification centres for the premaxilla, and attempts to show that each premaxilla is generated by two distinct centres for each side, altogether four distinct centres, in opposition to Kölliker's total of two.

Gilis, Allen

Gilis 1888 (62) describes a skull upon the palate of which an additional element of the premaxilla was situated—between the endognathic divisions of the premaxilla. This case, Gilis believes, tends to support the theory of a distinct separate element for the lodgement of each incisor tooth.

Allen 1890 (63) gives an interesting description, from his medical practice, of a number of cases of hyperostosis of the premaxillary portion of the nasal septum, which he describes as lying "anteriorly, between the triangular cartilage and the floor of the nose," that is to say, the vomerine portion of the premaxilla.

Osborn

Osborn 1892 (64), who is the "Cartwright Lecturer" referred to by Wood Jones upon an earlier page, writes "The human premaxillary, a discovery with which Goethe's name will always be associated, is sometimes partially, more rarely wholly, isolated; it is late to unite with the maxillary in the Australians, and has been reported entirely separate in a New Caledonian child (Deslongchamps) and in two Greenlanders (Carus)."

With respect to Deslongchamps' study 1866 (44) it is obvious from Hamy's (46) reference to it that Deslongchamps was referring chiefly to the palatine premaxillary suture, and not to the facial premaxillary suture. Carus' study it has been impossible to trace.

Sussdorf, Testut

Sussdorf 1895 (66) has a short but comprehensive discussion of the comparative anatomy of the premaxilla.

Testut's *Anatomie* 1899 (67) gives a short but comprehensive review of what was known of the premaxilla at that date, without reference, however, to the more obscure features of the bone.

Frison

The twentieth Century opens with a study of the premaxilla by Frison 1901 (68). In this work Frison treats of the human premaxilla from the pathological point of view, and he cites some twenty-six cases in which the premaxilla was the only bone in the skull to be affected by disease. Inflammation, and often exfolia-

tion, of the bone may, according to Frison, follow upon any of the eruptive fevers—particularly scarlatina, and may occur during any of the tertiary stages of syphilis. Frison accounts for this peculiar sequestration of the premaxilla in such diseases in the following way: The maxilla is composed of compact tissue, whereas the premaxilla is composed almost entirely of spongious bone. Spongious bone, it is well known, is less resistant to infection than compact bone. The premaxilla has an independent blood supply (the spheno-palatine) artery; when, then, infection occurs in the premaxilla the blood supply is very easily arrested, with the result that necrosis of the bone soon takes place.

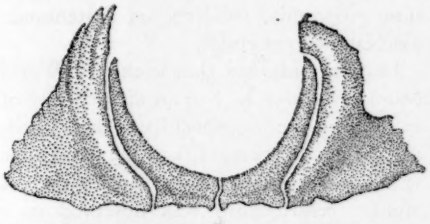

FIG. 3. SHOWING THE TWO HALVES OF THE PREMAXILLA COMPLETELY SEPARATED FROM THE MAXILLA IN A HUMAN FOETUS AT THE BEGINNING OF THE THIRD MONTH
After Ranke

Ranke

Ranke 1901 (69) in an interesting paper deals fairly exhaustively with the palatine portion of the premaxillary suture in the Primates. Among other things, he describes and figures the completely patent facial portion of the premaxillary suture in a human foetus of 28 mm., that is, at the beginning of the third month (Fig. 3).

Jeffery

Jeffery 1904 (71) reports the case of a young woman aged twenty years in whom the premaxilla was completely absent. In early life this young woman had been operated on for hare-lip, but at 20 there was still no bony union between the maxillae. In the canine portion of the maxilla Jeffery found what he describes as "a tiny tooth which might have been a relic of the lateral incisor"; he does not state, however, from which side of the maxilla this "relic" was removed.

Fischel

Fischel 1905 (72) described the skull of a middle-aged woman in which the premaxilla was either completely absent or only rudimentarily developed. The maxillary incisors were absent, and there was no anterior nasal spine. As a result of the absence of the premaxilla the palate assumed an unusual pyramidal form, being 37.0 mm. in length, 38.0 mm. broad posteriorly, and only 15.0 mm. broad between the alveoli of the first premolars. An anterior palatine foramen of more than usual dimensions was present which was bordered by the free margins of the maxillae. Fischel ascribed the absence of the premaxilla in this case to an early failure of development, but the evidence from the figures of the skull he describes suggest rather a post-natal pathological loss of the premaxilla.

Mosher

Mosher 1909 (76) considered the relation of the premaxilla to disorders in eruption of the maxillary incisors, prognathism, and deflection of the nasal septum. He considers merely the palatine and vomerine portions of the premaxilla. He finds that the premaxilla is less reduced in the negro than in the white, a fact which to some extent explains the alveolar incisorial prognathism of the negro. Mosher shows further, that deflection of the nasal septum may often be caused by the irregular or excessive growth of the vomerine portion of the premaxilla.

Le Double

Le Double 1906 (73) has a fairly full discussion of the premaxilla, but no conception of the form of the bone as a whole can be gained from it. Le Double notes that in the newborn and young chimpanzees the premaxillary facial suture is generally obliterated in its lower two-thirds; and that in the adult and old animals the suture is completely obliterated. It is interesting to note, he adds, that the disappearance of this suture occurs from below upwards as is the case in man.

The works of Rabl 1920 (70), Anderson 1908 (74), Preiswerk 1908 (75), Hopf 1909 (77), Bruni 1911/12 (79), and Frets 1912 (80), are of general interest in connection more particularly with the development and form of the palatine portion of the premaxilla in man and the remainder of the Primates; so too, are the works of Murakami 1928 (97), and Mijsberg 1928 (98).

Fawcett

Fawcett 1911 (78) in what is undoubtedly the most comprehensive original study of the maxilla and associated structures, states that he has never observed the facial portion of the premaxilla upon the face in embryos. In this study Fawcett gives, for the first time, a thorough explanation of the nature of the fissures which appear upon the oral surface of the premaxilla. "These" writes Fawcett "are due to the fact that the backs of the two incisor teeth are early covered, each of them, by down-growths of bone from the premaxillary mass; and these coverings, not only growing downwards, but at the same time backwards, produce elevations which imperfectly meeting, result in intervening fissures."

Inouye

Inouye 1912 (81) has published the most exhaustive study of the premaxilla in man in existence. This study is a very long one. Possibly the most important fact in this work, from our point of view, is the author's description of the persistence of the superior portion of the premaxillary suture upon the face in a one year old child. A drawing of the skull is given by Inouye. Of the condition he writes,

> Wie Fig. 3 deutlich zeigt, beginnt die Naht an der Mitte des Seitenrandes des Nasenbeines, läuft dann auf dem Processus frontalis des Oberkiefers parallel seinem medialen freien Rande, um nach einem ziemlich langen Verlaufe in einem kleinen Gefässloche zu verschwinden; die Länge der Sutur beträgt 1.3 cm. Der Verlauf dieser Naht entspricht genau dem der zur Furche geschlossenen Sutur, die bereits auf der nasalen Fläche des Stirnfortsatzes des Oberkiefers beim Kinde besehen worden ist.

Thus, it is to be observed "dass die nasale Sutura incisiva nicht am Rande der Apertura piriformis, sondern am Seitenrande des Nasenbeines endet. . . "

Inouye points out that in the Old World Monkeys which he had an opportunity of examining the relationship of the ascending process of premaxilla to the nasal bone is similar to the human condition. A similar relationship was observed in a young orang, though in the gorilla the ascending process terminated at the superior pyriform aperture.

Bolk

Bolk 1913 (82) in his lengthy work on the obliteration of the sutures in the primate skull, gives a detailed report of his findings with respect to the premaxillary suture. His conclusions, briefly summarised, are as follows: Obliteration begins in the

> Foetal period in Man, Chimpanzee.
> Infantile period in *Cebus*, *Chrysothrix*, Orang.
> Juvenile period in Siamang.
> Mature period in *Macacus* ♂, Gorilla, *Cercopithecus*
> Adult period in *Alouatta*, *Ateles*, *Hapale*, *Semnopithecus* ♂ *and* ♀, *Cynocephalus*, *Colobus*

Bolk thinks that there is probably some relationship between the degree of prog-

nathism displayed by any Primate and the period at which obliteration of the premaxillary suture takes place.

Walker

Walker 1917 (83) reports a case of absence of the premaxilla in an English boy aged 14 years. Walker's own summary of the case is as follows:

1. The case shows complete absence of the premaxilla, with the four upper incisors and deficient ossification of the nasal septum. Other malformations are absent.

2. The two maxillary processes have grown forwards and inwards, have met each other and the nasal septum in the mesial plane, carrying the canines into the incisor portion, and have filled the space left by the pre-maxilla.

3. The history of the case is open to doubt, but it suggests that the premaxilla was sloughed at the age of three during an attack of measles. A previous deficiency of attachment must be supposed. Congenital defect of the mesial nasal process is evidenced by the condition of the existing nasal septum.

Richardson

Richardson 1918 (84) reports the case of a young man, aged 26, who complained of intense pain in the floor and lateral wall of the left nasal chamber. In order to relieve the pain the four maxillary incisors were removed, but in a short time the premaxilla became entirely necrosed and separated from the maxilla in a single mass. Richardson cites as an important and salient feature of this case the fact of the complete limitation within distinct anatomic borders of the bony necrosis, affecting only the premaxilla. In the discussion of this paper Dr. H. L. Swain refers to a precisely similar case which came under his notice.

Felber, Jarmer, Herbst

Felber 1919 (86), and Jarmer 1922 (87) have independently investigated the embryological development of the premaxilla in man; their conclusions are in substantial agreement. They are in agreement that the centers for the premaxillary bones first make their appearance at the beginning of the seventh week of development, slightly after the appearance of the ossification centers for the maxilla, and that by the conclusion of the twelfth week the facial portions of the premaxillary bones become completely united with the maxilla.

Herbst 1923 (88) has a very thoroughgoing discussion of the premaxilla in relation to the varieties of hare-lip and cleft palate.

Bercher and Merville

Bercher and Merville 1923 (89) and (90) report four cases of necrosis of the premaxilla occurring during the tertiary stages of syphilis in four adult soldiers. In each case all the marked characters of congenital syphilis were present.

Bercher 1924 (91) comments upon the predisposition of the premaxillaries to disease in such disorders as syphilis and the eruptive fevers.

Vallois and Cadenat

Vallois and Cadenat 1924 (92) examined the premaxillary region in 30 human foetuses between the second and seventh months of development; they write:

Le prémaxillaire est visible pour la première fois sur un embryon de 21 mm., c'est un petit noyau situé en avant de la lame dentaire, dans la région qui correspond aux futures incisives. Très rapidement, il se soudé à celui du maxillaire qui est apparu plustôt et occupe la future région molaire. L'union des deux centres forme une lame osseuse qui borde en dehors la lame dentaire.

À 41 mm., cette lame envoie en haut 2 prolongements, l'un correspondant à sa portion maxillaire, l'autre a sa portion prémaxillaire; ce sont les processus frontaux. Le processus frontal du prémaxillaire borde, par son bord antérieur, l'orifice nasal. Son bord postérieur est longé par le processus frontal du maxillaire, dont un interstice le sépare. A 44 mm le prémaxillaire; et son process frontal, bien développés, constituent une lame compacte qui s'étend de la gouttière vestibulaire à l'os nasal. La face interne (bucco-nasale) de cette lame se prolonge en dedans par un tissu osseux à mailles l'âches, qui forme le fond

et la paroi linguale des alvéoles des incisives et s'enfonce dans la partie correspondante du palais dont il constitute le squelette. C'est le prolongement palatine du prémaxillaire. Sa partie la plus interne émet une petite languette qui se dirige d'avant en arrière, le long de la ligne médiane. Par homologie avec la disposition des animaux, on peut l'appeler processus palatin médian. Tout le reste du prolongement sera lors dit processus palatin latéral. Dans l'échancrure qui sépare les 2 processus passe le canal de Stenson.

En arrière, une suture très nette, la suture incisive, sépare le prolongement analogue émis par la maxillaire. Au cours du 4e mois, se produisent certains changements. Le processus frontal du maxillaire, d'abord situé en arrière de celui du prémaxillaire, pousses en dehors de lui une lame qui recouvre en partie sa face externe. En même temps, les 2 processus se soudent l'une à l'autre, mais le trace de la séparation primitive reste encore visible sur leurs faces externe et interne. Le processus palatin latéral s'accroît notablement; c'est maintenant une épaisse lame qui forme toute la partie de la voûte palatine correspondant aux incisives; son bord postérieur, bilobé, limite la suture incisive. . . .

Au cours des 5e & 6e mois, le prémaxillaire perd la plus grande partie de son indépendance. Son apophyse frontale est presque totalement recouverte en dehors par l'apophyse frontale du maxillaire et lui est complètement soudée. Sur la face externe, la ligne de suture est visible pendant quelques temps comme un fin sillon qui longe dehors le pourtour de l'orifice nasal. Sur le face interne, la ligne de suture est plus postérieur; elle disparaît de bas en haut, la soudure débutant au niveau du cornet inférieur.

Thus, it seems clear from both Callender's and Vallois' and Cadenat's observations that the premaxillary suture disappears upon the facial aspect of the human skull early in development because the premaxilla becomes completely, or almost completely, covered by the facial process of the maxilla, with which it apparently becomes indissolubly united, although, as Vicq D'Azyr long ago showed, the suture upon the internum of the maxilla may persist late into the post-natal development of the individual. Superficially understood this manner of development may be construed to be appreciably different from that which takes place in the sub-human Primates, and, indeed, there certainly exists a difference in the *degree* of development, but not in the *kind*. For, as we shall see, the present form and structure of the premaxilla in man represent the expression of an active process of the involution which this bone has for a considerable period of time been undergoing as a result of the important series of changes which have taken place in the oral-olfactory life of man.

Remane

Remane 1927 (96) investigated the period of closure of the premaxillary suture in the anthropoid apes. For the chimpanzee he finds that "Bei allen Individuen, auch den jüngsten, ist der untere Teil der fazialen Naht verschlossen," and this always before birth. The suture is in most cases already obliterated at the conclusion of the juvenile period. In the gorilla the suture is found persistent in most adults. In the orang two structurally dimorphic groups are recognisable with respect to the period of obliteration, although no sexual difference is discoverable. In the first "beginnt der Verschluss bald nach Vollendung des Milchgebisses." In the second "wachst die Intermaxillarnaht kurz vor Vollendung des Dauergebisses." In the gibbon "treffen wir denselben Dimorphismus wie beim Orang in noch verstärkten Form an." Remane's conclusions are as follows with respect to the period of obliteration:

Beim Schimpansen, als enzigem Primaten ausser dem Menschen, beginnt der Verschluss regelmässig vor der Geburt. Der Abschluss der Obliteration liegt jedoch nicht selten nach Vollendung des Dauergebisses. (Innere palatinaler Teil).

Der Gorilla verschliesst bis auf seltene Ausnahmefälle die Naht erst zur Zeit oder kurz nach Vollendung des Dauergebisses. Der Orang und die Hylobatiden zeigen einen Dimorphismus, ein Teil der Tiere beginnt mit dem Verschluss zur Zeit der Vollendung

des Milchgebisses oder kurz nachher, ein anderer erst kurz vor Vollendung des Dauergebisses

With respect to the manner of obliteration Remane writes, "Beim Schimpanse und Gibbon der Verschluss direkt am Alveolarrand dehnt sich von hier z.T. etappenweise sowohl auf die faciale wie auf die palatinale Naht aus; beim Gorilla und noch mehr beim Orang beginnt er fazial ein Stück oberhalb des Alveolarrandes, palatinal in der Regel im Zwischenteil."

Ehrhardt

Ehrhardt 1930 (103) examined the large collection of anthropoid crania at Munich in order to check Remane's conclusions. She finds that "der Mensch und der Schimpanse haben von den Anthropomorphen das relativ am schwächsten entwickelte Gebiss, beide zeigen den frühen Nahtverschluss." Her conclusions are,

I. Die ersten Verwachsungentreten beim Orang-Utan und Gibbon mit Vollendung des Milchgebisses und kurz nachher, vermutlich auch kurz vorher, auf. Die Zahl der Schädel, die noch in Beginn der Verwachsung stehen, nimmt mit steigender Altersstufe allmählich ab. Die ersten Schädel mit vollkommen verschlossener Naht treten beim Orang-Utan in V., beim Gibbon in der IV. Altersstufe auf. (IV. Beginnender bis nahezu vollendeter Durchbruch von Eckzahn und letztem Molar. V. Gebiss vollendet). Beim Orang-Utan und Gibbon verwachst die Sutura incisiva *kontinuierlich*, im Verwachsen zeigt sich kein Dimorphismus.

II. Beim Gibbon verwächst die Sutura incisiva früher als beim Orang-Utan.

With respect to the manner of obliteration:

I. Beim Orang-Utan beginnt die Verwachsung faciale, etwas oberhalb der Alveole. Der faciale Teil verwächst, abgesehen von nasalen Nahtresten, früher als der palatinale.

II. Beim Gibbon (*Hylobates concolor*) beginnt zuerst der palatinale Teil alveolar zu verwachsen. Der faciale Teil schliesst sich jedoch auch hier früher.

III. Beim Siamang (*Symphalangus syndactylus*) erfolgt der Verschluss als *Hylobates concolor*, nur der faciale Teil verwächst an der Alveole später.

Ehrhardt notes that obliteration of the premaxillary suture in the Orang and Gibbon takes place earlier in the female than in the male.

Herbst and Apffelstaedt

Herbst and Apffelstaedt 1930 (104) have an excellently clear discussion of the relation of the premaxilla to the varieties and forms of cleft palate and hare-lip.

Krogman

Krogman 1930 (105) in a study of suture-closure in the Primates, states that the premaxillary generally closed about the time of eruption of the first permanent molar in the gibbon, about the time of eruption of the deciduous teeth in the orang, rather earlier in the chimpanzee, and in the pre- or early adult period in the gorilla. In *Papio hamadryas* the suture undergoes obliteration not before the adult period. With respect to *Pithecus rhesus*, he agrees with Bolk (82) "that closure of these sutures starts in the male in the pre-adult period (eruption of second molar), and that in the female they are always patent."

Augier

Augier 1932 (110) has recently published an extremely interesting study of the premaxilla based upon his observations of the conditions in early human embryos. He states that the two maxillary centers appear at the 15 mm. stage, whilst the premaxillary centers appear at the 26 mm. stage, and generally unite with the maxilla at the 30 mm. stage. Augier writes "La soudure précoce des centres maxillaires humains est en rapport avec leur régression." This regression may be re-

garded as a result of the unique orthognathism of the human face.

Nous sommes hypothétiquement persuadés que ce temps d'apparation est le même chez tous les Primates, parce que chez l'Homme, où la réduction est la plus marquée, le prémaxillaire reste aussi précoce qu'il puisse être (c'est le troisième centre céphalique).

Chez trois animaux (Homme, Cochon, Cobaye) où l'architecture bucco-nasale diffère beaucoup, mais où l'importance dentaire du prémaxillaire reste grande, nous voyons ce centre apparaître d'une facon à Peu près comparable (Mandibule, Postmaxilla, Prémaxilla, Frontal chez le premier; Mandibule, Postmaxilla, Frontal, Prémaxilla chez les deux autres). Chez le Mouton (malgré un materiél abondant, nos résultats restant provisoires), où l'architecture faciale diffère *relativement* peu de celle des deux autres Quadrupèdes, mais où l'importance dentaire (Nous ne disons pas buccale) de cet os est nulle, son centre apparaît un peu plus tardivement; le prémaxillaire semble y être le quatrième ou le cinquième ou le sixième centre céphalique."

Augier concludes "que c'est le développement plus ou moins précoce des dents qui décide du développement plus ou moins précoce du prémaxillaire."

Limson

Limson (1932) (111) examined the macerated skulls of 142 white and negro foetuses, in addition to 32 infants ranging in age from birth to 2 years of age, the purpose being to record "the many significant variations in the bones of the skull during the fetal and early infantile periods of development." Of the premaxilla Limson writes,

In all the fetal and infantile skulls the intermaxillary is completely fused with the maxillary bone on the outer surface, but is entirely separated from it on the oral surface by means of the sutura incisiva. This suture was invariably found to extend from the foramen incisivum to the interalveolar septum between the lateral incisor and canine. The same suture is also visible on the floor of the nasal cavity and proceeds, at least in prenatal growth stages, for some distance along the inner surface of the ascending process. It is very interesting that this suture between maxillary and intermaxillary is not only regularly present on the lateral wall of the fetal nasal cavity, but lies closer to the margo lacrimalis than to the lateral edge of the apertura piriformis, indicating an unexpectedly broad nasal process of the intermaxillary bone. As stated above, no trace of this ascending suture could be detected on the outer surface of even the youngest fetal skulls examined.

Franz

Franz (1933) (115), a short time after this paper was completed, published an extremely important paper bearing upon the whole question of Goethe's premaxillary contributions. It seems quite clear from Franz' discoveries that Goethe was aware of Vicq D'Azyr's publication of six years antecedent to his own, but for some mysterious reason preferred to keep silent concerning it. For a full discussion of the matter the reader should refer to Franz' splendid paper.

Summary of the literature

This concludes our survey of the literature dealing with the premaxilla; it may be summarised in the following words:

The human premaxilla is a bone of very definite form and structure, it is a perfect homologue of the equivalent structure possessed by the lower mammals. The bone undergoes ossification from at least two distinct centers, which appear first during the seventh week of development, when after, according to its observers, at or about the end of the twelfth week of development the facial portion of the premaxilla apparently becomes completely or almost completely overgrown, or overlaid, by a plate of ossificatory material, originating in the matrix of the maxilla, with which it subsequently becomes more or less inseparably united. It is clear too, that in some cases the premaxilla may persist in its entirety, ununited to the maxilla, as a distinct and independent

entity, or that it may be entirely absent, produced, or retracted owing to disease or failure of development, and finally, that it may become sharply sequestrated from the adjacent bones following upon local inflammation or disease.

The premaxilla, it is observed, is composed of two bilaterally symmetrical units, each consisting of three arbitrary but easily recognisable parts, namely, a *body*, a *palatine process*, and an *ascending* or *naso-maxillary process*.

Inferiorly each body contributes towards the support of the two incisor teeth (to what extent I shall show later). From the body arise two processes, the palatine and the ascending or naso-maxillary processes. The palatine process plays a part in the formation of the anterior moiety of the palate and the floor of the nasal cavity, and also helps to form the incisive foramen, finally, upon its narial surface giving rise to a keel-like process which helps to complete the vomer anteriorly. The naso-maxillary process contributes towards the formation of the whole extent of the internal anterolateral boundaries of the pyriform aperture.

(To be concluded)

EXPERIMENTAL STUDIES ON THE DURATION OF LIFE. XIV. THE COMPARATIVE MORTALITY OF CERTAIN LOWER ORGANISMS

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I

THE first complete life tables based upon comprehensive and accurate observations for any other organism than man, were, so far as we know, those published in the first of this series of Studies by Pearl and Parker (30) in 1921 for normal wild-type *Drosophila melanogaster*, and for its mutant *vestigial*. Since that time partial or complete life tables for *Drosophila* have been published by Pearl and Parker (31) for line-bred strains; (32) showing effect of successive etherizations; (33) demonstrating influence of density of population on duration of life; (34) influence of ventilation and of feeding embryonic juice; (35) re-computed life tables; (36) for duration of life in the complete absence of food. Pearl, Parker and Gonzalez (37) have published life tables on the Mendelian inheritance of duration of life in *Drosophila*, and on the effect of surgically removing the wings upon duration of life. Gonzalez (12) computed *Drosophila* life tables showing the relation of certain mutant genes to duration of life; Pearl, Miner and Parker (29) on the effect of density of population; Alpatov and Pearl (2) on the effect of temperature; Alpatov (1) on the effects of feeding; and Steinfeld (43) on the effects of a sterile environment. For other non-human forms the following life tables have been published: for the saturniid moth *Telea polyphemus* a graph of the ungraduated survivorship line by Pearl and Parker (35) based on data published by Philip and N. Rau (40); for the rotifer *Proales decipiens* by Pearl and Doering (26) based on data published by Noyes (19); and for mice by Greenwood (14) based on data from Leonard Hill and J. A. Murray. Data on life duration without the computation of life tables have also been given by Hase (16) for the common *Hydra fusca;* by Rau (39) for the roach *Blatta orientalis;* and by the Szabós (45) for the slug *Agriolimax agrestis*. Recently Gardner and Hurst have published life tables for the domestic fowl (10). Certain of these data, not previously graduated, have been fitted with the following equations:

Hydra fusca:

$$\log_{10} 1000\, q_x = 1.053 + 0.052\, x - 0.0059\, x^2 + 0.00023\, x^3$$

(Origin at 2 days; x unit = 5 days)

Agriolimax agrestis:

$$\log l_x = \epsilon^{-0.0416x}\,(3 - 0.0248\, x + 0.0283\, x^2 - 0.0031\, x^3)$$

Blatta orientalis:

$$\log_{10} l_x = 1.188^x\,(3 - 0.525\, x + 0.059\, x^2 - 0.016\, x^3)$$

(Origin at 0 days; x unit = 15 days)

Starved wild (Line 107) *Drosophila:*

$$l_x = \frac{1100}{1 + 0.100\epsilon^{0.0075x} + 0.00000077\epsilon^{0.32x}}$$

(Origin at 0 hours; x unit = 1 hour)

Starved vestigial *Drosophila:*

$$l_x = \frac{1000.1}{1 + 0.00001000\epsilon^{-.1960x} + 0.000000001820\epsilon^{+.4126x}}$$

TABLE 1

Complete life table for Hydra fusca

AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$
days					*days*					*days*				
0	1000	11	10.8	54.9	50	476	7	16.2	39.4	100	175	5	32.0	16.7
1	989	11	11.0	54.5	51	469	8	16.2	39.1	101	170	6	33.3	16.2
2	978	11	11.3	54.1	52	461	8	16.2	38.7	102	164	6	34.6	15.7
3	967	11	11.6	53.7	53	453	7	16.2	38.3	103	158	5	36.1	15.3
4	956	11	11.8	53.3	54	446	7	16.2	37.9	104	153	6	37.6	14.8
5	945	12	12.1	53.0	55	439	7	16.3	37.6	105	147	6	39.3	14.4
6	933	11	12.3	52.6	56	432	7	16.3	37.2	106	141	6	41.1	14.0
7	922	12	12.6	52.2	57	425	7	16.3	36.8	107	135	5	43.1	13.5
8	910	11	12.8	51.9	58	418	7	16.4	36.4	108	130	6	45.0	13.1
9	899	12	13.1	51.6	59	411	7	16.4	36.0	109	124	6	47.1	12.7
10	887	12	13.3	51.3	60	404	6	16.4	35.6	110	118	6	49.3	12.3
11	875	12	13.5	50.9	61	398	7	16.5	35.1	111	112	5	51.5	11.9
12	863	12	13.7	50.6	62	391	6	16.5	34.7	112	107	6	53.9	11.5
13	851	12	13.9	50.3	63	385	7	16.6	34.3	113	101	6	56.4	11.2
14	839	11	14.1	50.0	64	378	6	16.7	33.9	114	95	5	59.0	10.8
15	828	12	14.2	49.7	65	372	6	16.8	33.4	115	90	6	61.7	10.4
16	816	12	14.4	49.4	66	366	6	16.8	33.0	116	84	5	64.5	10.1
17	804	11	14.6	49.1	67	360	7	16.9	32.6	117	79	6	67.5	9.8
18	793	12	14.7	48.9	68	353	6	17.0	32.1	118	73	5	70.6	9.4
19	781	12	14.8	48.6	69	347	6	17.2	31.7	119	68	5	73.8	9.1
20	769	11	15.0	48.3	70	341	5	17.3	31.2	120	63	5	77.2	8.8
21	758	12	15.1	48.0	71	336	6	17.4	30.7	121	58	5	80.8	8.5
22	746	11	15.2	47.8	72	330	6	17.6	30.3	122	53	4	84.5	8.2
23	735	11	15.3	47.5	73	324	6	17.7	29.8	123	49	4	88.4	7.9
24	724	11	15.4	47.2	74	318	5	17.9	29.3	124	45	4	92.4	7.6
25	713	11	15.5	46.9	75	313	6	18.1	28.9	125	41	4	96.7	7.3
26	702	11	15.6	46.7	76	307	6	18.3	28.4	126	37	4	101.1	7.1
27	691	11	15.7	46.4	77	301	5	18.5	27.9	127	33	4	105.8	6.8
28	680	11	15.7	46.1	78	296	6	18.8	27.4	128	29	3	110.6	6.6
29	669	10	15.8	45.9	79	290	5	19.0	26.9	129	26	3	115.7	6.3
30	659	11	15.9	45.6	80	285	6	19.3	26.5	130	23	3	121.0	6.1
31	648	10	15.9	45.3	81	279	5	19.6	26.0	131	20	2	126.6	5.8
32	638	10	15.9	45.0	82	274	6	20.0	25.5	132	18	3	132.4	5.6
33	628	10	16.0	44.8	83	268	5	20.3	25.0	133	15	2	138.5	5.4
34	618	10	16.0	44.5	84	263	6	20.7	24.5	134	13	2	144.8	5.2
35	608	10	16.0	44.2	85	257	5	21.1	24.0	135	11	1	151.5	5.0
36	598	9	16.1	43.9	86	252	5	21.5	23.5	136	10	2	158.5	4.8
37	589	10	16.1	43.6	87	247	6	22.0	23.0	137	8	1	165.7	4.6
38	579	9	16.1	43.3	88	241	5	22.4	22.5	138	7	1	173.4	4.4
39	570	9	16.1	43.0	89	236	6	23.0	22.1	139	6	1	181.3	4.2
40	561	9	16.1	42.7	90	230	5	23.5	21.5	140	5	1	189.7	4.0
41	552	9	16.1	42.4	91	225	6	24.1	21.0	141	4	1	198.4	3.8
42	543	9	16.2	42.1	92	219	5	24.8	20.5	142	3	1	207.5	3.7
43	534	9	16.2	41.8	93	214	5	25.5	20.0	143	2	0	217.0	3.5
44	525	8	16.2	41.5	94	209	6	26.2	19.5	144	2	1	227.0	3.3
45	517	9	16.2	41.1	95	203	5	27.0	19.1	145	1	0	237.4	3.2
46	508	8	16.2	40.8	96	198	6	27.9	18.6	146	1	0	248.3	3.0
47	500	8	16.2	40.5	97	192	5	28.8	18.1	147	1	0	259.8	2.8
48	492	8	16.2	40.1	98	187	6	29.8	17.6	148	1	1	271.7	2.7
49	484	8	16.2	39.8	99	181	6	30.9	17.1					

The above curves are purely empirical and make no pretense to stating any "laws" of life. They are computed solely for the purpose of accurately and systematically smoothing the raw data of the irregularities consequent upon random sampling and experimental errors.

The complete life tables for *Hydra fusca*, *Agriolimax agrestis*, *Blatta orientalis*, and starved wild (Line 107) *Drosophila* males, and starved vestigial *Drosophila* males are given in Tables 1–5 inclusive. In these tables l_x denotes the number alive at the beginning of each age interval; q_x denotes the rate of mortality, i.e., the number dying in the age interval per thousand living at the beginning of the interval; and $\mathring{e}_x$ denotes the expectation of life, i.e., the average length of life remaining to each individual alive at the beginning of the interval. It is to be understood that in these tables the original experimental observations for *Hydra*, *Agriolimax*, and *Blatta* are accepted as valid on the evidence presented by the authors cited in each case. In the case of *Drosophila* the experimental work was done in this laboratory and we accept full responsibility.

TABLE 2.

Complete life table for Agriolimax agrestis

AGE	l_x	d_x	$1000q_x$ (PER 0.2 MONTH)	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$ (PER 0.2 MONTH)	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$ (PER 0.2 MONTH)	$\mathring{e}_x$
months				*months*	*months*				*months*	*months*				*months*
0	1000	64	63.9	4.09	5.0	393	16	40.9	2.61	10.0	42	6	142.4	1.12
0.2	936	55	58.8	4.16	5.2	377	16	43.5	2.51	10.2	36	5	147.4	1.08
0.4	881	48	54.2	4.22	5.4	361	17	46.3	2.42	10.4	31	5	152.3	1.05
0.6	833	41	48.8	4.26	5.6	344	17	49.2	2.34	10.6	26	4	157.2	1.03
0.8	792	37	46.0	4.27	5.8	327	17	52.3	2.25	10.8	22	4	162.2	1.00
1.0	755	32	42.5	4.27	6.0	310	17	55.7	2.17	11.0	18	3	167.1	0.97
1.2	723	28	39.4	4.26	6.2	293	18	59.0	2.09	11.2	15	2	172.0	0.95
1.4	695	26	36.7	4.23	6.4	275	17	62.7	2.02	11.4	13	2	177.0	0.93
1.6	669	23	34.2	4.19	6.6	258	17	66.3	1.95	11.6	11	2	181.9	0.90
1.8	646	21	32.3	4.13	6.8	241	17	70.2	1.88	11.8	9	2	186.8	0.88
2.0	625	19	30.6	4.07	7.0	224	17	74.0	1.81	12.0	7	1	191.7	0.86
2.2	606	17	29.3	3.99	7.2	207	16	78.2	1.75	12.2	6	1	196.6	0.84
2.4	589	17	28.3	3.91	7.4	191	15	82.3	1.69	12.4	5	1	201.4	0.82
2.6	572	16	27.6	3.82	7.6	176	15	86.6	1.63	12.6	4	1	206.3	0.80
2.8	556	15	27.3	3.73	7.8	161	15	90.9	1.57	12.8	3	1	211.1	0.79
3.0	541	15	27.2	3.63	8.0	146	14	95.3	1.52	13.0	2	0	215.9	0.77
3.2	526	14	27.4	3.53	8.2	132	13	99.8	1.47	13.2	2	1	220.6	0.75
3.4	512	14	27.9	3.42	8.4	119	13	104.3	1.43	13.4	1	0	225.3	0.74
3.6	498	15	28.7	3.31	8.6	106	11	109.0	1.38	13.6	1	0	230.0	0.72
3.8	483	14	29.7	3.21	8.8	95	11	113.7	1.34	13.8	1	0	234.7	0.71
4.0	469	14	31.0	3.11	9.0	84	10	118.3	1.30	14.0	1	1	239.2	0.69
4.2	455	15	32.5	3.00	9.2	74	9	123.1	1.26					
4.4	440	16	34.4	2.90	9.4	65	8	127.9	1.22					
4.6	424	15	36.3	2.80	9.6	57	8	132.8	1.18					
4.8	409	16	38.5	2.70	9.8	49	7	137.6	1.15					

II

In their first paper Pearl and Parker (30) made a rough comparison of *Drosophila* and human life tables, basing their comparison on the equating of one day of fly life to one year of human life. In a later paper Pearl (20) returned to this question, basing his comparison on a superposing of the two curves

so that at least two *biologically equivalent* points coincide. The best two points would be the beginning and the end of the life span. But in the case of *Drosophila* our life tables start with the beginning of *imaginal* life only. The larval and pupal durations are omitted.

Pearl therefore took for his starting point the age "*when the instantaneous death rate q_x is a minimum.*" This was taken to be the life span cannot be satisfactorily determined; the most straightforward approximation to it is the age at which only some small fraction of the original cohort is left alive. In later papers comparisons by the same method were made by Pearl and Doering (26) of the mortality of *Proales* with those of *Drosophila* and man, and by

TABLE 3

Complete life table for Blatta orientalis

AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$
days					*days*					*days*				
0	1000	1	1.1	40.9	25	902	15	16.1	18.3	50	232	25	111.0	6.4
1	999	1	1.0	39.9	26	887	16	18.0	17.6	51	207	25	117.3	6.1
2	998	1	0.7	39.0	27	871	17	19.9	16.9	52	182	22	123.9	5.8
3	997	0	0.6	38.0	28	854	19	22.0	16.2	53	160	21	130.7	5.6
4	997	1	0.6	37.0	29	835	20	24.3	15.6	54	139	19	137.6	5.4
5	996	1	0.5	36.0	30	815	22	26.7	14.9	55	120	18	144.9	5.1
6	995	0	0.6	35.1	31	793	23	29.3	14.3	56	102	15	152.4	4.9
7	995	1	0.6	34.1	32	770	25	32.0	13.8	57	87	14	160.1	4.7
8	994	1	0.7	33.1	33	745	26	34.8	13.2	58	73	12	168.0	4.5
9	993	1	1.0	32.1	34	719	27	37.8	12.6	59	61	11	176.3	4.3
10	992	1	1.3	31.2	35	692	28	41.0	12.1	60	50	9	184.7	4.2
11	991	1	1.6	30.2	36	664	30	44.3	11.6	61	41	8	193.4	4.0
12	990	2	2.0	29.2	37	634	30	47.9	11.1	62	33	7	202.2	3.8
13	988	3	2.5	28.3	38	604	31	51.5	10.7	63	26	5	211.4	3.7
14	985	3	3.2	27.4	39	573	32	55.4	10.2	64	21	5	220.8	3.5
15	982	4	3.9	26.5	40	541	32	59.4	9.8	65	16	4	230.4	3.4
16	978	4	4.6	25.6	41	509	32	63.7	9.4	66	12	3	240.3	3.3
17	974	6	5.5	24.7	42	477	33	68.1	9.0	67	9	2	250.3	3.1
18	968	6	6.4	23.8	43	444	32	72.8	8.6	68	7	2	260.6	3.0
19	962	7	7.5	23.0	44	412	32	77.6	8.2	69	5	1	271.2	2.9
20	955	8	8.6	22.1	45	380	31	82.6	7.9	70	4	1	281.9	2.8
21	947	10	9.9	21.3	46	349	31	87.9	7.6	71	3	1	292.9	2.7
22	937	10	11.2	20.5	47	318	30	93.3	7.2	72	2	1	304.1	2.6
23	927	12	12.8	19.8	48	288	28	99.0	6.9	73	1	0	315.5	2.5
24	915	13	14.3	19.0	49	260	28	104.9	6.6	74	1	0	327.1	2.4
										75	1	1	338.9	2.3

age 1 day for *Drosophila* and age 12 years for man. As an approximation to the indeterminate upper end of the life span was taken the age "at which there is left but *one* survivor out of 1,000 starting at age 1 day for *Drosophila* and age 12 years for white males." There is, of course, an arbitrary element in this, as in most approximations. The exact upper end of Pearl and Parker (35) of wild type and vestigial *Drosophila* with man and with *Telea polyphemus*.

This method of comparing life tables of different organisms has been criticised by Greenwood (14) on the ground that the sampling error will be high for the age at which there is left one survivor out of a thousand. Brownlee (5) assumed that

TABLE 4

Life table for starved wild (Line 107) Drosophila melanogaster

AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$
hours					*hours*					*hours*				
0	1000	1	0.7	44.1	25	980	2	1.5	19.7	50	158	38	237.5	3.5
1	999	0	0.7	43.1	26	978	1	1.8	18.7	51	120	29	245.9	3.4
2	999	1	0.7	42.1	27	977	2	2.1	17.8	52	91	23	252.3	3.3
3	998	1	0.7	41.2	28	975	3	2.6	16.8	53	68	18	257.2	3.3
4	997	0	0.7	40.2	29	972	3	3.3	15.9	54	50	13	260.9	3.3
5	997	1	0.7	39.2	30	969	4	4.2	14.9	55	37	10	263.7	3.2
6	996	1	0.7	38.3	31	965	6	5.4	14.0	56	27	7	265.8	3.2
7	995	1	0.7	37.3	32	959	6	7.1	13.0	57	20	5	267.3	3.2
8	994	0	0.7	36.3	33	953	9	9.4	12.1	58	15	4	268.4	3.2
9	994	1	0.7	35.3	34	944	12	12.4	11.2	59	11	3	269.2	3.2
10	993	1	0.7	34.4	35	932	15	16.4	10.4	60	8	2	269.8	3.2
11	992	0	0.7	33.4	36	917	20	21.8	9.5	61	6	2	270.2	3.2
12	992	1	0.7	32.4	37	897	26	28.8	8.7	62	4	1	270.6	3.2
13	991	1	0.8	31.4	38	871	33	37.8	8.0	63	3	1	270.8	3.2
14	990	1	0.8	30.5	39	838	41	49.0	7.3	64	2	0	271.0	3.2
15	989	1	0.8	29.5	40	797	50	62.8	6.6	65	2	1	271.1	3.2
16	988	0	0.8	28.5	41	747	59	79.1	6.0	66	1	0	271.2	3.2
17	988	1	0.8	27.5	42	688	68	97.8	5.5	67	1	0	271.3	3.2
18	987	1	0.9	26.5	43	620	73	118.2	5.1	68	1	1	271.3	3.2
19	986	1	0.9	25.6	44	547	76	139.5	4.7					
20	985	1	0.9	24.6	45	471	76	160.5	4.3					
21	984	1	1.0	23.6	46	395	71	180.5	4.1					
22	983	1	1.1	22.6	47	324	64	198.5	3.9					
23	982	1	1.2	21.7	48	260	56	214.0	3.7					
24	981	1	1.3	20.7	49	204	46	227.0	3.6					

TABLE 5

Life table for starved vestigial (mutant) Drosophila melanogaster

AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$	AGE	l_x	d_x	$1000q_x$	$\mathring{e}_x$
hours				*hours*	*hours*				*hours*	*hours*				*hours*
0	1000	0	0.02	44.8	25	987	3	2.9	20.1	50	225	49	216.9	3.4
1	1000	0	0.03	43.8	26	984	3	3.5	19.2	51	176	41	235.2	3.3
2	1000	0	0.03	42.8	27	981	5	4.3	18.2	52	135	34	251.8	3.1
3	1000	0	0.04	41.8	28	976	5	5.2	17.3	53	101	27	266.6	3.0
4	1000	0	0.05	40.8	29	971	6	6.3	16.4	54	74	21	279.2	2.9
5	1000	0	0.05	39.8	30	965	7	7.6	15.5	55	53	15	290.0	2.8
6	1000	0	0.07	38.8	31	958	9	9.2	14.6	56	38	12	299.0	2.7
7	1000	0	0.09	37.8	32	949	11	11.2	13.7	57	26	8	306.5	2.7
8	1000	0	0.1	36.8	33	938	12	13.6	12.9	58	18	5	312.6	2.6
9	1000	1	0.1	35.8	34	926	16	16.4	12.1	59	13	4	317.4	2.6
10	999	0	0.1	34.8	35	910	18	19.9	11.2	60	9	3	321.6	2.6
11	999	0	0.2	33.8	36	892	21	24.1	10.5	61	6	2	324.8	2.5
12	999	0	0.2	32.8	37	871	26	29.1	9.7	62	4	1	327.4	2.5
13	999	0	0.3	31.8	38	845	29	35.1	9.0	63	3	1	329.4	2.5
14	999	1	0.3	30.8	39	816	35	42.3	8.3	64	2	1	331.2	2.5
15	998	0	0.4	29.8	40	781	40	50.8	7.6	65	1	0	332.5	2.5
16	998	1	0.5	28.8	41	741	45	60.9	7.0	66	1	0	333.6	2.5
17	997	0	0.6	27.9	42	696	50	72.6	6.4	67	1	1	334.5	2.5
18	997	1	0.7	26.9	43	646	56	86.1	5.9					
19	996	1	0.9	25.9	44	590	60	101.4	5.4					
20	995	1	1.1	24.9	45	530	62	118.5	5.0					
21	994	1	1.3	23.9	46	468	65	137.1	4.6					
22	993	2	1.6	23.0	47	403	63	156.9	4.2					
23	991	2	2.0	22.0	48	340	60	177.1	3.9					
24	989	2	2.4	21.1	49	280	55	197.4	3.7					

the imaginal life of *Drosophila* is equivalent to the total postnatal life of man.

Feeling the inadequacy of Pearl's earlier method of comparing the order of dying with respect to age of different organisms, not only because of the defect pointed out by Greenwood but also for other reasons, we have sought to find a more trustworthy method. We believe that it is available in the fact that the method devised by Pearl (22) for representing relative variability may be applied to the comparison of life tables of different organisms, each of which differs in the absolute duration of its life span. Each table, on this plan, *may be presented in terms, not of years or of days or any other absolute time ut,ni but of percentage deviations from the mean duration of life*. The values of the mean durations of life for the organisms compared are given in Table 6.

TABLE 6
Mean duration for life tables discussed

LIFE TABLES	MEAN DURATION OF LIFE
Drosophila, Normal wild type ♂♂	45.81 days
Drosophila, Vestigial ♂♂	14.13 days
Drosophila, Normal wild type, starved ♂♂	44.09 hours
Drosophila, Vestigial, starved ♂♂	44.77 hours
Proales decipiens	5.95 days
Hydra fusca	54.89 days
Blatta orientalis	40.89 days
Agriolimax agrestis	4.12 months
Mice (Hill's data)	636.5 days
Automobiles	7.04 years

This method of comparison will not be subject to Greenwood's criticism, since the mean is one of the most efficient of statistics. In its determination all the observed data play a part. The mean or average is, of course, basically a statistical concept—an abstraction used to define, in part, the characteristics of a group. But it has long been an accepted biological generalization that the mean may be taken more satisfactorily than any other abstraction yet suggested as representing the *type* of the species. There would seem to be no reason why this generalization should not be as valid for duration of life as for other measurable characters. The mean duration of life for species *A* tells us how long the individuals of that species *typically* live. This information, in common sense and reason, is surely comparable and has the same meaning from species to species.

Table 7 gives, for ages expressed as percentage deviations from the mean duration of life (a) the survivorship distributions (l_x) of the various organisms, together with Griffin's (15) automobile life table; (b) the death distributions (d_x) of the same groups; and (c) the death rate distributions (1000 q_x per 20 percent deviation from the mean duration of life) of the same groups.

The nature and meaning of the results embodied in Table 7 will be clearer if they are exhibited in graphic form. This is done in Figs. 1, 3, and 5.

III

Let us examine first the survivorship curves of Table 7 and Fig. 1. These give the number of survivors at the same relative ages out of each 1000 born (or starting their life histories) together. It is at once clear that the ten curves fall naturally into three groups or classes. These groups we have called respectively the rectangular, intermediate, and diagonal. They represent different *types* of life tables, or, otherwise stated, different types of distribution in relative time of the relative number of survivors. The first of these types, the *rectangular, in the theoretical limiting case* describes the situation where all the individuals in a cohort are born at the same time, live for the same length of time, and all die at the same instant of time. The l_x curve for such a cohort

TABLE 7

Survivorship (l_x), death (d_x), and death rate ($1000q_x$ per 20 per cent deviation) distributions expressed as percentage deviations from mean duration of life

SPECIES AND DISTRIBUTION	PERCENTAGE DEVIATIONS FROM MEAN DURATION OF LIFE																	
	−100	−80	−60	−40	−20	0	+20	+40	+60	+80	+100	+120	+140	+160	+180	+200	+220	+240
Drosophila (*Wild type. Line 107*) ♂♂																		
Survivorship (l_x)	1000	988	945	867	741	556	322	118	19	1	—	—	—	—	—	—	—	—
Death (d_x)	12	43	78	126	185	234	204	99	18	1	—	—	—	—	—	—	—	—
Death rate (q_x)	12	44	83	145	250	421	634	839	947	1000	—	—	—	—	—	—	—	—
Drosophila (*Vestigial*) ♂♂																		
Survivorship (l_x)	1000	993	924	795	635	469	323	211	132	84	49	30	18	11	5	2	—	—
Death (d_x)	7	69	129	160	166	146	112	79	52	31	19	12	7	6	3	2	—	—
Death rate (q_x)	7	69	140	201	261	311	347	374	394	387	388	400	389	545	600	1000	—	—
Drosophila (*Starved wild type*) ♂♂																		
Survivorship (l_x)	1000	991	981	967	914	537	71	5	—	—	—	—	—	—	—	—	—	—
Death (d_x)	9	10	14	53	377	466	66	5	—	—	—	—	—	—	—	—	—	—
Death rate (q_x)	9	10	14	55	412	868	930	1000	—	—	—	—	—	—	—	—	—	—
Drosophila (*Starved vestigial*) ♂♂																		
Survivorship (l_x)	1000	1000	997	981	895	544	81	3	—	—	—	—	—	—	—	—	—	—
Death (d_x)	0	3	16	86	351	463	78	3	—	—	—	—	—	—	—	—	—	—
Death rate (q_x)	0	3	16	88	392	851	963	1000	—	—	—	—	—	—	—	—	—	—
Agriolimax agrestis																		
Survivorship (l_x)	1000	787	664	583	519	460	398	330	259	190	129	81	46	24	11	5	2	1
Death (d_x)	213	123	81	64	59	62	68	71	69	61	48	35	22	13	6	3	1	1
Death rate (q_x)	213	157	122	108	114	136	171	215	266	320	375	429	481	530	576	617	655	688
Hydra fusca																		
Survivorship (l_x)	1000	875	747	629	526	440	367	302	242	182	119	59	18	3	—	—	—	—
Death (d_x)	125	128	118	103	86	73	65	60	60	63	60	41	15	3	—	—	—	—
Death rate (q_x)	125	146	158	164	163	166	177	199	248	346	504	695	833	1000	—	—	—	—
Proales decipiens																		
Survivorship (l_x)	1000	1000	996	967	849	543	147	1	—	—	—	—	—	—	—	—	—	—
Death (d_x)	0	4	29	118	306	396	146	1	—	—	—	—	—	—	—	—	—	—
Death rate (q_x)	0	4	29	122	360	729	993	1000	—	—	—	—	—	—	—	—	—	—
Blatta orientalis																		
Survivorship (l_x)	1000	994	977	908	752	513	258	83	15	1	—	—	—	—	—	—	—	—
Death (d_x)	6	17	69	156	239	255	175	68	14	1	—	—	—	—	—	—	—	—
Death rate (q_x)	6	17	71	172	318	497	678	819	933	1000	—	—	—	—	—	—	—	—
Mus (Hill's data)																		
Survivorship (l_x)	1000	988	961	901	775	548	247	40	1	—	—	—	—	—	—	—	—	—
Death (d_x)	12	27	60	126	227	301	207	39	1	—	—	—	—	—	—	—	—	—
Death rate (q_x)	12	27	62	140	293	549	838	975	1000	—	—	—	—	—	—	—	—	—
Automobiles																		
Survivorship (l_x)	1000	979	912	801	654	488	325	191	94	38	12	3	—	—	—	—	—	—
Death (d_x)	21	67	111	147	166	163	134	97	56	26	9	3	—	—	—	—	—	—
Death rate (q_x)	21	68	122	184	254	334	412	508	596	684	750	1000	—	—	—	—	—	—

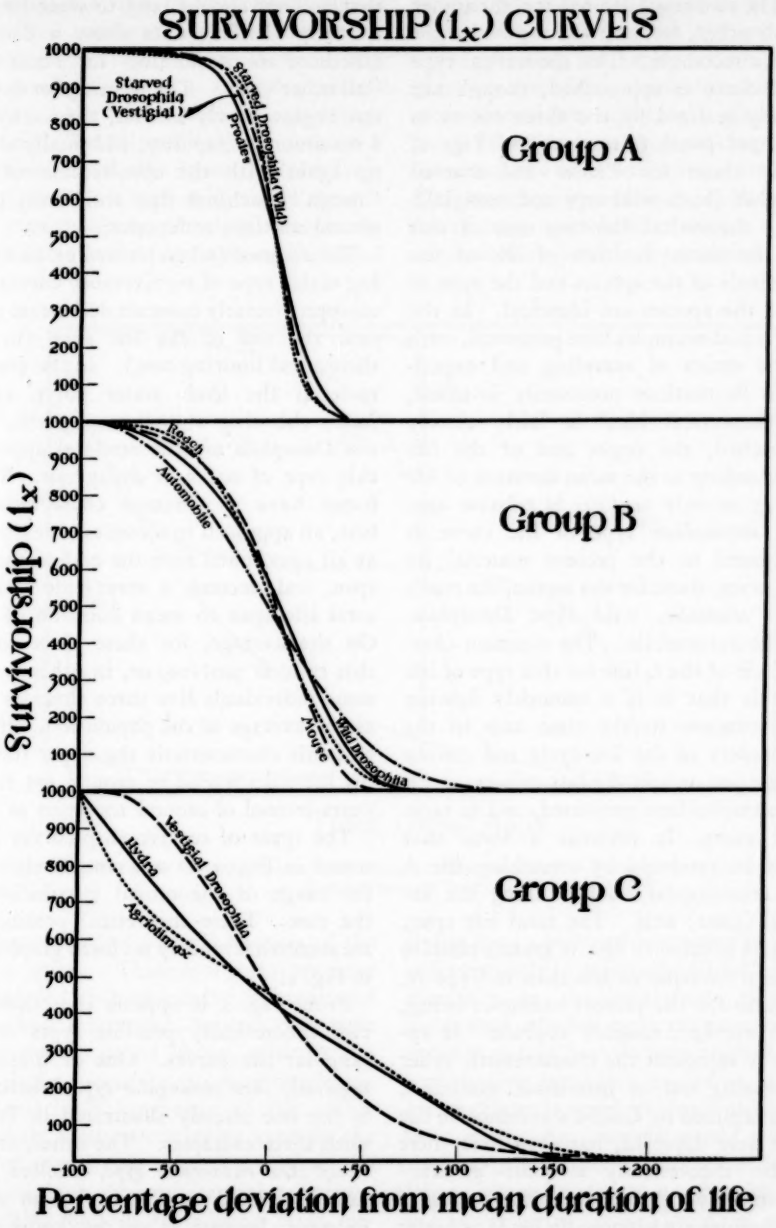

FIG. 1. SURVIVORSHIP CURVES FOR VARIOUS SPECIES OF ANIMALS AND FOR AUTOMOBILES ON A RELATIVE TIME BASE
For each form represented the mean duration of life is taken as 100 percent on the abscissal scale, and all other ages (time duration) are expressed as percentage deviations (plus or minus) from this mean.

would be two straight lines at right angles to each other, forming the top and right side of a rectangle. This theoretical type of life curve is approached, though not precisely realized by the three curves in the upper panel (Group A) of Fig. 1, namely those for *Proales* and starved *Drosophila* (both wild type and vestigial). In the theoretical limiting case of this type the mean duration of life of the individuals of the species and the span of life of the species are identical. In the three actual examples here presented, with all the errors of sampling and experimental fluctuations necessarily involved, this theoretical ideal is fairly closely approached, the upper end of the life span standing to the mean duration of life roughly as only 140:100 in relative age.

An *intermediate* type of life curve is represented in the present material by four curves, those for the mouse, the roach *Blatta orientalis*, wild type *Drosophila*, and the automobile. The common characteristic of the l_x line for this type of life curve is that it is a smoothly flowing curve concave to the time axis in the first moiety of the life cycle and convex to the same axis in the last moiety, in all the examples here presented, and in most other cases. It presents a form that might be produced by stretching the A type (rectangular) l_x line along the abscissal (time) axis. The total life span, in terms of relative age, is greater relative to mean duration of life than in Type A, the ratio for the present examples being, as an average, roughly 185:100. It appears to represent the characteristic order of wearing out of man-made machines, as exemplified by Griffin's automobile life curve here depicted, but even here there is also theoretically a quasi-"genetic" element, since more expensive types of automobiles are supposedly made of better materials than the cheaper types, and on that account should tend to wear longer. Actually Griffin's data show a distinct difference in the l_x lines for Fords and "all other" cars. The wearing (or dying) out begins slowly at first, then achieves a maximum of rapidity, and finally slows up again with the obsolescence of the "tough" machines that stubbornly hang on and continue to function.

The *diagonal* (when plotted on an arith-log scale) type of survivorship curves has an approximately constant death-rate until near the end of the life span (in the theoretical limiting case). In the present material the fresh water polyp *Hydra fusca*, the slug *Agriolimax agrestis*, and the *Drosophila* mutant vestigial approach this type of order of dying out. These forms have as common characteristics, first, an approach to a constant death-rate at all ages, until near the end of the life span, and, second, a very wide ratio of total life span to mean duration of life. On the average, for these three forms, this ratio is 300:100, or, in other words, some individuals live three times as long as the average of the population. If man had this characteristic the upper limit of his life span would be around 175 to 180 years instead of around 100 years as it is.

The types of survivorship curves illustrated in Fig. 1 do not completely cover the range of theoretical possibilities in the case. These theoretical possibilities are somewhat crudely set forth graphically in Fig. 2.

From Fig. 2 it appears that there are two theoretically possible types of rectangular life curves. One of these, the *negatively skew rectangular type*, labelled A, is the one already illustrated in Fig. 1, with three examples. The other, or *positively skew rectangular type*, labelled D, is not illustrated in Fig. 1 by an actual example, because as yet we know of no living organism that very closely ap-

proaches this type in the distribution of its normal survivorship. The nearest approach to this type that we know of, and this is admittedly not a very close approach, is the life table for human beings in India [See Glover (11) p. 261, or a reproduction of this figure in Pearl (25), p. 245]. In this type of life curve there is an extremely heavy mortality immediately after birth (or the beginning of life) that eliminates all but a small fraction of the whole cohort. These few survivors must be regarded as biologically differentiated from those eliminated, because they have the power to go on living, with only a very slight mortality, to the completion of a relatively long span of life. This positively skew rectangular type is the sort of curve that would represent the most extreme type of natural selection. Something closely resembling it is frequently brought about by artificial selection as practiced by live-stock breeders. For example, many years ago when we were operating an experimental poultry plant at the Maine Agricultural Experiment Station we might, in a given year, hatch from 3000 to 5000 chicks, and in three months or so kill off (or otherwise eliminate from the cohort) all but 500 or 600 to carry over the next winter. These selected birds would, if permitted, go on living for a considerable number of years, suffering only a relatively slight natural mortality in the meantime. While a good case of this type of survivorship curve in nature has not been studied with quantitative precision, so far as we are aware, there is good evidence that such cases exist. An example would presumably be pelagic breeding types of teleost fishes, where enormous numbers of eggs and larval forms are produced, of which only relatively few survive, but those

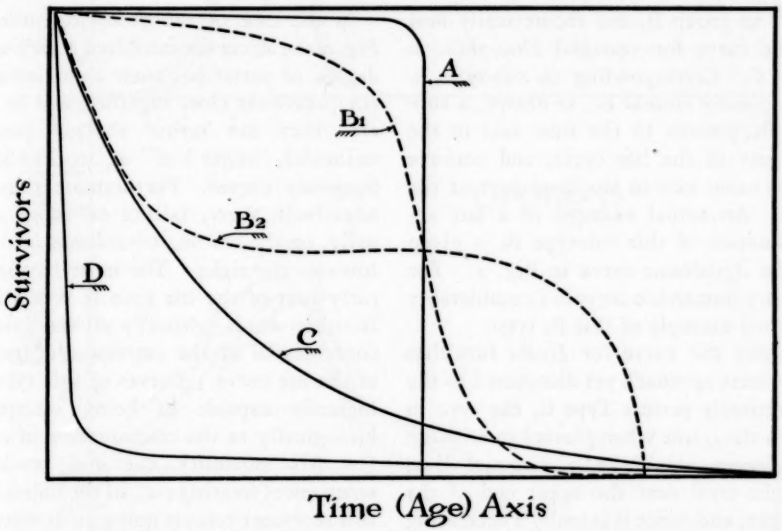

FIG. 2. DIAGRAM TO ILLUSTRATE THE THEORETICALLY POSSIBLE DISTINCT TYPES OF LIFE CURVES. EXPLANATION IN TEXT

that do survive have a long life span. Szabó (44) cites as example of this general type of curve that furnished by the mortality of forest trees, and illustrates it specifically by the data of Fekete (9) on the oak. But the curve as pictured by him is far from an extreme illustration of the type.

From Fig. 2 it seems clear that what we called group B (*Intermediate*) is really only a sub-type, now labelled B_1 of our Type C. Sub-type B_1 is represented in Fig. 1 by the curves in group B, and theoretically best by the curve for vestigial *Drosophila* in Panel C. Corresponding to sub-type B_1 there plainly should be, as drawn, a sub-type B_2, convex to the time axis in the first part of the life cycle, and concave to the same axis in the later part of the cycle. An actual example of a fair approximation of this sub-type B_2 is given by the *Agriolimax* curve in Fig. 1. The ordinary human life curve is a considerably distorted example of this B_2 type.

Finally the curve for *Hydra* furnishes the nearest approach yet discovered to the theoretically perfect Type C, the type in which the l_x line when plotted to arithlog coördinates would be a diagonal line, straight until near the upper end of the life span; and, since it is really a decreasing exponential, when plotted to arithmetic coördinates, a gently curving diagonal line convex to the base.

We turn next to the consideration of the death curves (d_x) of Table 7. These are shown graphically in Fig. 3.

The discussion of the death curves may well be prefaced by the remark that, with the exception of the automobile, in all the forms dealt with in Table 7, d_x (in the true actuarial sense) is *directly* observed, and is in fact the basic observation from which all the other life table functions are derived. Each individual in each group is observationally followed throughout its life, from its birth to its death.

We see at once from Fig. 3 that the death curves are essentially *frequency curves of variation* relative to time of dying. They show the distribution of individual variations in the duration of life from birth to death. They differ among themselves in respect of

a. Scatter (degree of inter-individual variation), and

b. Skewness.

In the case of the group A curves of Fig. 3 the d_x curves exhibited a very small degree of variation; their two limbs are comparatively close together, and in general they are rather sharply peaked, unimodal, "sugar loaf" or "cocked hat," frequency curves. Furthermore they are negatively skew, tailing off more gradually, on the whole, towards the left than towards the right. The mortality in the early part of the life span is very slight. In other words, virtually all the dying is concentrated at the extreme old age end of the life curve. Curves of this type are logically capable of being interpreted biologically as the consequences of *either*:

1. All mortality the end result of senescence (wearing out) of the individual, this senescent process going on at virtually the same time rate and to the same degree in each individual of the species, or

2. All mortality the result of a lethal agent of environmental origin, so powerful that its ability to kill considerably transcends individual variations in power to resist its action, with the result that it kills all the individuals at the same time. Thus, for example, if a somewhat greater than minimum lethal dose of a poison were given to all the individuals of a cohort born at the same time the result would be a life curve of the A type. Precisely this sort of thing is what did happen in the case of two starved *Drosophila* curves,

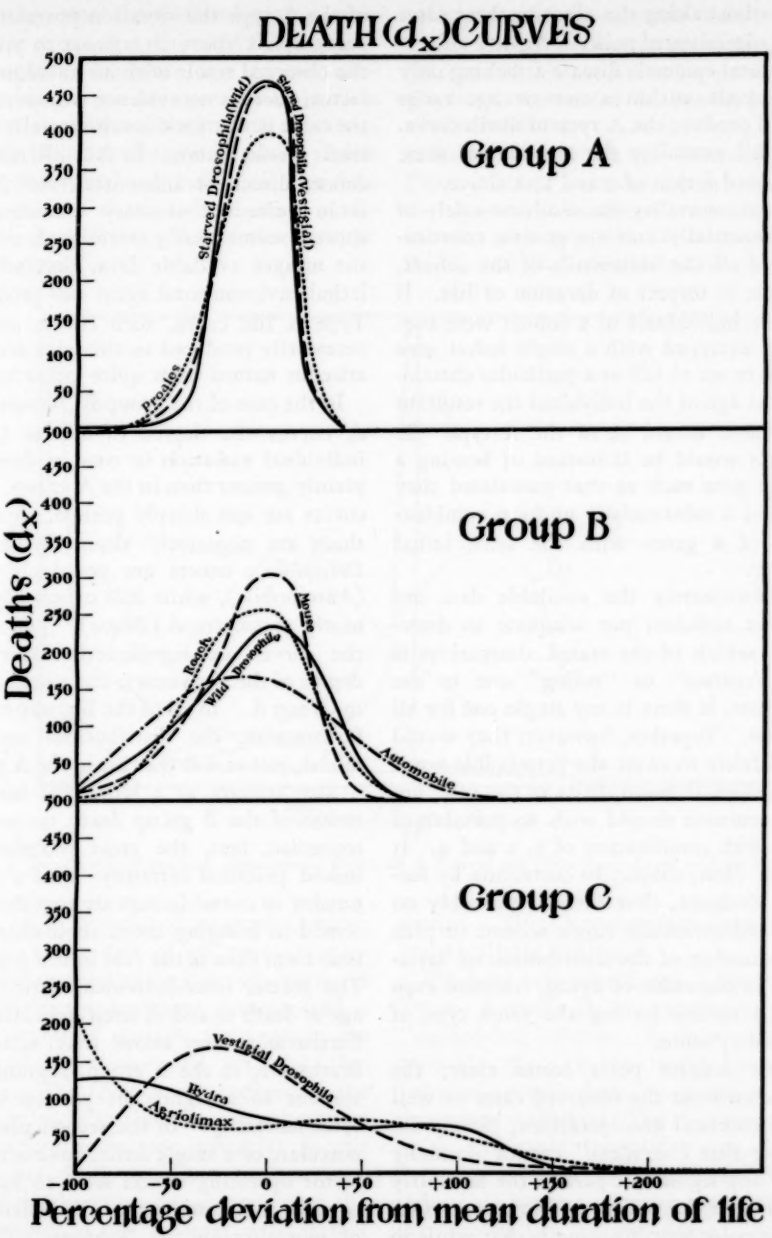

FIG. 3. DEATH CURVES FOR VARIOUS SPECIES OF ANIMALS AND FOR AUTOMOBILES ON A RELATIVE TIME BASE
For each form represented the mean duration of life is taken as 100 percent on the abscissal scale, and all other ages (time duration) are expressed as percentage deviations (plus or minus) from this mean.

starvation taking the place in these cases of an administered poison. Again a universally fatal epidemic disease attacking only individuals within a narrow age range would produce the A type of death curve.

3. All mortality the resultant of some combined action of 1 and 2 as above.

4. All mortality the resultant solely of a substantially uniform genetic constitution of all the individuals of the cohort, specific in respect of duration of life. If all the individuals of a cohort were supposed equipped with a single lethal gene timed or set to kill at a particular chronological age of the individual the resultant life curve would be of the A type. So also it would be if instead of bearing a single gene such as that postulated they all had a substantially uniform combination of n genes with the same lethal power.

Unfortunately the available data are neither sufficient nor adequate to determine which of the stated alternatives is the "correct" or "ruling" one in the premises, if there is any single one for all species. Together, however, they would seem fairly to cover the permissible range of biological possibilities in the case, unless someone should wish to postulate a final fifth combination of 1, 2 and 4. It is our view, subject to correction by further evidence, that there is probably no one and invariable single scheme or plan of causation of the distribution of variation in the order of dying, common even to all species having the same type of mortality table.

One definite point seems clear; the evidence from the observed cases as well as theoretical considerations, plainly indicate that "accident" cannot normally play any significant part in the mortality leading to the A type of life curve. One other point worth noting is that while in the case of the starved *Drosophila* curves of the A type the situation postulated in paragraph 2 above is *sufficient* to produce the observed result without an additional factor, there is no evidence whatever that the same is true for the substantially identical *Proales* curve. In fact all the evidence, direct or inferential, for *Proales* is in quite the contrary direction. In short it seems clearly established, even on the meager available data, that while a lethal environmental agent *will* produce a Type A life curve, such curves are not necessarily produced in this way but *may* arise in nature from quite other causes.

In the case of the group B (*Intermediate*) d_x curves the degree of scatter (inter-individual variation in time of dying) is plainly greater than in the A group. The curves are less sharply peaked. Some of them are negatively skew (Wild type *Drosophila*), others are positively skew (Automobile), while still others are very nearly symmetrical (*Blatta*). But where the curves are significantly skew, the degree of the skewness is less marked than in Group A. In all of the B group curves, furthermore, the distributions are unimodal, just as was the case in the A group.

Any attempt at a biological interpretation of the B group death curves will recognize, first, the great probability—indeed practical certainty—that a larger number of causal factors are together concerned in bringing about their characteristic form than is the case in the A group. The greater inter-individual variation in age at death in and of itself indicates this. Furthermore we know that accidental deaths are, in the B group, beginning to amount to a significant portion of the total mortality. In the second place the postulate of a single lethal environmental factor operating would seem to have no cogency in accounting for the distribution of mortality in the B group. The individuals are widely scattered in their time

of dying, and the peak of mortality is neither at nor near the end of the life span. As regards senescence and genetic constitution, it would seem probable that insofar as either of these is in operation it must be less uniform in its rate of action from individual to individual, or less homogeneous from individual to individual, in producing B type than A type death curves.

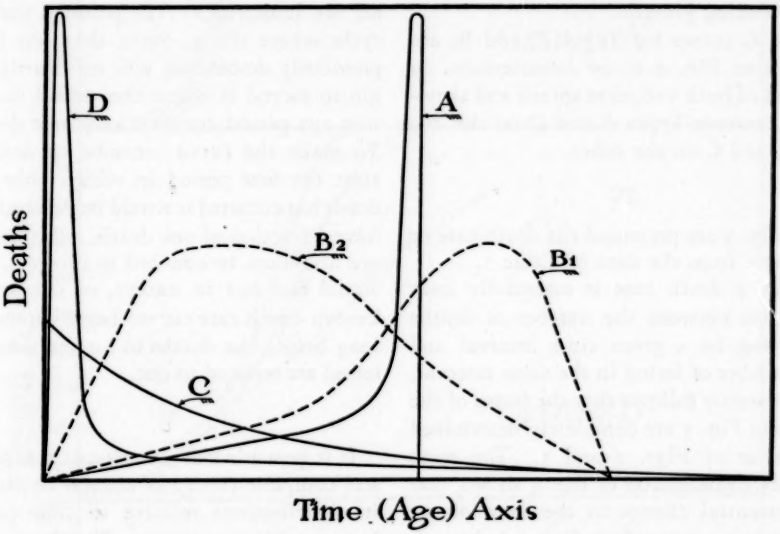

FIG. 4. DIAGRAM ILLUSTRATING THEORETICAL FORMS OF d_x CURVES FOR FOUR BASIC TYPES OF LIFE CURVES

The characteristics of the group C curves of Fig. 3 are, first of all great inter-individual variability in time of dying—in fact relatively enormous scatter—and a great degree of positive skewness in the cases of *Agriolimax* and vestigial *Drosophila*. The *Hydra* curve approaches the rectangular or straight horizontal type of frequency distribution, indicating in this case a practically constant absolute number of deaths per unit of time over the greater part of the life span, until in fact the numbers of living in the pool from which the deaths occurred has been so reduced near the extreme upper end of the life span that it is no longer possible for the constant number of deaths per unit of time to occur.

Turning from the actual examples of Table 7 let us consider briefly what are the theoretical limiting forms of d_x curves for our basic types of life curves A, B_1, B_2, C, and D discussed in the preceding section. These limiting forms are shown graphically in Fig. 4.

We have represented the d_x curves for Types A and D as extremely skew "cocked-hat" curves. It is at least as probable that at the limits these are J-shaped curves, with, of course, a finite maximum ordinate. The C type curve is an extremely interesting one, for it depicts a situation where the age of the individual has *per se* nothing to do with the probability of its dying. By inference these are forms in which neither

senescence nor genetic constitution play any significant rôle. That there are such forms has been ably argued by Bidder (3, 4). Mortality in such cases is wholly a consequence of the direct action of environmental forces, and is "accidental" from the standpoint of the organism. Bidder argues that forms behaving relative to mortality in this way are characteristically aquatic organisms and that the absence of senescence is associated with never ending growth.

The d_x curves for Types B_1 and B_2 are seen from Fig. 4 to be intermediate, in respect of both variation spread and skewness, between Types A and D on the one hand, and C on the other.

IV

In Fig. 5 are presented the death-rate or q_x curves from the data of Table 7.

Since a death rate is essentially only the ratio between the number of deaths occurring in a given time interval and the number of living in the same interval, it necessarily follows that the forms of the curve in Fig. 5 are completely determined by those of Figs. 1 and 3. The most cursory examination of Fig. 5 shows that the essential change in the form of the q_x curves as we pass from Group A through B to C is generally *decreasing* rapidity of slope upward of the lines, or, conversely, an increasing tendency of the q_x line to approach horizontality until the upper end of the life span is nearly approached.

Theoretically the q_x curve, from a starting value at birth, may either (a) generally ascend, (b) stay approximately horizontal, (c) generally descend, or (d) pursue a sinuous course, falling in the first part of the life span and rising in the latter part. Actually the *general* trend of all q_x curves so far observed is ascending either throughout the whole life span or in its later portions. Man and *Agriolimax* are the only forms so far quantitatively studied in which the q_x curve definitely descends even during the first part of the life span. In *Hydra* the curve is very nearly horizontal for the whole first half of the life span. For purely arithmetic reasons, as has been intimated earlier in this paper, the q_x curve must necessarily ascend towards the end of the life span in any species with a finite life span (that is, in which the individuals composing it are not immortal). The point in the life cycle where the q_x curve that has been previously descending will necessarily begin to ascend is where the second successive age period contains only one death. To make the curve continue to descend after the first period in which only one death has occurred it would be necessary to have a fraction of one death. But deaths are and must be counted in integers. In actual fact and in nature, of course, all known death rate curves begin ascending long before the deaths in a given time interval are reduced to one.

V

Is it possible now to present a rational and complete theory of natural death and its distributions relative to time (age)? In our opinion it is not. The data available to build upon are far too meager. Counting in man, we have reasonably complete life tables for only some seven species of animals, and these few species differ widely among themselves in respect of their order of dying out. All that we can sensibly hope to do in the present state of knowledge, as it seems to us, is to carry the rational biological analysis of the problem as far as possible, and then await more data before going further. This we shall now try briefly to do. The views to be developed combine some features of theories that have been advanced by various workers. While for the sake

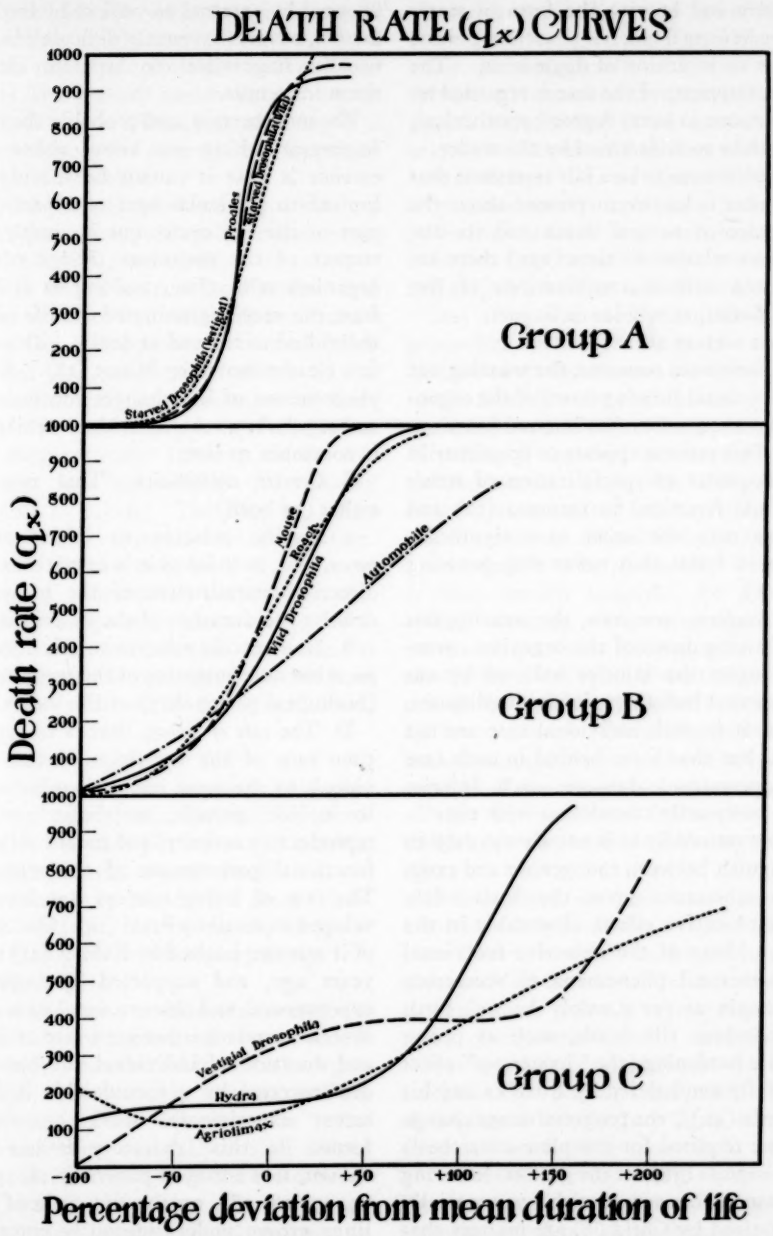

FIG. 5. DEATH RATE CURVES FOR VARIOUS SPECIES OF ANIMALS AND FOR AUTOMOBILES ON A RELATIVE TIME BASE

For each form represented the mean duration of life is taken as 100 percent on the abscissal scale, and all other ages (time duration) are expressed as percentage deviations (plus or minus) from this mean.

of clarity and brevity the form of statement is in form dogmatic at certain points, there is no intention of dogmatism. The whole statement of the case is regarded by us at present in some degree hypothetical, and is to be so understood by the reader.

It would seem to be a fair statement that in all that is known at present about the occurrence of natural death and its distribution relative to time (age) there are concerned various combinations of five major *factors*, as wholes or in part.

These factors are:

A. *Endogenous senescence*, the wearing out and functional slowing down of the organism in consequence of its internal functioning. This process appears to be primarily a consequence of specialization of structure (and function) in metazoa (21) and perhaps may not occur to a significant degree in forms that never stop growing (Bidder).

B. *Exogenous senescence*, the wearing out and slowing down of the organism consequent upon the injuries inflicted by environmental buffetings, infectious diseases, etc., that in each individual case are not lethal, but that leave behind in each case some permanent damage; such injuries being necessarily cumulative with time.

Observationally it is not always easy to distinguish between endogenous and exogenous senescence upon the basis solely of the objective effects observable in the body. Many of the objective functional and structural phenomena of senescence that begin at (or possibly before) birth and continue till death, such as protoplasmic hardening (the "hysteresis" effect especially emphasized by Růžička and his students (42)), the progressive age change in time required for complete anaesthesia in *Drosophila* (38), or the gradual lowering of the metabolism rate with age, especially emphasized by Child (6) are matters that well may be and probably are in part influenced by external as well as by internal factors, but it is extremely difficult—in fact usually impossible—to separate clearly these influences.

The most certain, and probably the most important, thing we know about senescence is that it cannot be sharply delimited to particular ages or a particular part of the life cycle, but is simply one respect of the *continuous* change of the organism with time, as long as it lives from the very beginning of the life of the individual to the end at death. This was first clearly shown by Minot (18). Every phenomenon of life changes continuously and regularly as the individual exhibiting it continues to live.

C. *Genetic constitution*. This may be either (or both)

a. Specific relative to life duration *per se*, and, in so far as it is operative at all, directly determinative of the particular definite life duration of the individual, or

b. Non-specific relative to life duration *per se* but determinative of the constitution (biological personality) of the individual.

D. The *rate of living*, that is to say the time rate of the activities of the individual, in the most comprehensive sense, to include growth, metabolic activity, reproductive activity, and indeed all other functional performance of the organism. The rate of living concept has been developed in detail by Pearl (24). One aspect of it was emphasized by Rubner (41) many years ago, and supported by ingenious experimental and observational data. The inverse correlation between rate of living and duration of individual life has been demonstrated by a considerable body of recent experimental work on various forms. In this laboratory it has been shown, in a series of papers (7, 8, 13, 23, 24, 27, 28, 38), on the life cycle of seedlings grown under rigorously controlled conditions, that duration of life is nega-

tively correlated with rate of growth. MacArthur and Baillie (17) have shown a similar negative correlation between longevity and general metabolic activity in *Daphnia magna*. That rate of living is a major factor in determining longevity admits of no doubt.

E. *Immediately lethal accidents*, including all major catastrophic environmental stoppages of the individual life.

There would seem to be abundant and cogent evidence that the items enumerated above and called *factors* in natural death are real and pertinent elements in the production and the distribution of mortality. It seems impossible to dispute that they are major factors. Of the five the first four are wholly or primarily *biological* in nature. The fifth is at first glance wholly environmental in its nature. But this is not completely so, because biological constitution plays some rôle in determining the incidence of accidents.

It is our hypothesis that there are but two fundamental biological *variables* concerned in death and its time distribution. These are:

a. *Genetic constitution*, and

b. *Activity*, in the broadest biological sense of the term, including not only motor activity, but such phenomena as growth, reproduction, and others as well.

To these is to be added a third fundamental variable, not necessarily or essentially biological in its nature, namely

c. *Environment*.

Thus we have as determinative of the life duration of the individual one variable internal and inherent relative to the organism (a), one variable external to the organism (c), and one (b) that in its quantitative expression is related to and in a sense determined by the interactions of (a) and (c).

In our view the rates of both endogenous and exogenous senescence (factors A and B) are determined by the interaction of these three variables. An individual may grow physiologically old slowly, and because it has such an extremely sound genetic constitution that it can withstand severe environmental buffeting and a high rate of living. Or, on the other hand, an objectively similar result may be attained by an individual of poor constitution that is fortunate in respect of its environment, and maintains a low rate of living.

One of several profound difficulties in proceeding further in a rigorous rational analysis of the problem of life duration lies in the fact that none of the three fundamental variables involved can, as wholes, be precisely measured or stated in quantitative terms. It is true that *elements* of the environment of a living individual, rather narrowly delimited both spatially and in time, can be measured. The same is true, *mutatis mutandis*, for an individual's activity. We can measure some particular activities during more or less short time. But what is wanted is a measure of the individual's *total* activities of all sorts, over its *whole* life; and also a numerical expression that will serve as a measure of net integrated effectiveness of *all* the environmental forces that have acted upon the individual throughout its life.

If and when we have such measures available there will be a better chance than there is now of reaching a rational theory of life duration. In the meantime it seems to us that the crying need is for more observational data, carefully and critically collected for different species of animals and plants, that will follow through the life history from birth to death of each individual in a cohort of statistically respectable magnitude. From such data sound and biologically meaningful life tables can be constructed. Work of this character, laborious as it is,

is likely to be more fruitful of real knowledge than the construction of any mathematical "law" of mortality, however ingenious. For it appears clear that there is no one universal "law" of mortality. The data discussed in the present paper are sufficient to show that different species may differ in the age distribution of their dying just as characteristically as they differ in their morphology.

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RESULTS IN THE PHYLOGENY OF A GENUS OF SNAILS

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A PAPER recently published by me (1932) treats of the phylogeny of the European representatives of *Viviparus* or *Paludina*. Under these names is comprehended a widely distributed and notable genus of prosobranch freshwater gastropods (snails). The number of its subgenera is about a dozen. Many of them at present live in Asia. The subgenus *Viviparus s. str.*, however, inhabits every part of the globe, and is the only one in Europe. It occurs in North America chiefly in the Missouri and Mississippi regions and in Cuba, without mentioning that the European species *Viviparus viviparus* in some localities has been imported by man. The other North American genera are *Campeloma* (*Melantho*), *Lioplax*, and *Tulotoma*, the latter only in Alabama. In South America are to be found only fossils, in Central America neither fossil nor living species have yet been discovered.

In spite of the limitation of my investigations to the European species (fossil and recent), several results, I think, will be of some interest from a more biological point of view.

Chronological and, as one may therefore suppose, phylogenetic seriations of the shells could be made on the basis of the general shapes of the shells, but not so extensively on the basis of the shapes of the apex (or vertex: acute, obtuse, or subacute) nor of the varying thickness of the shells, and not at all on that of the finer sculpture (i.e. principally the vestiges of the spines which occur on young (neonate) shells, and which, when broken off, leave either very small tubercles, or pits, upon a greater or smaller number of the whorls).

THE GENEALOGY OF THE GENUS VIVIPARUS

The phylogenetic seriation, which surely does not represent lines from ancestors to descendants, begins with *Viv. beaumontianus* in upper freshwater Cretaceous deposits of the South of France—since it is not certain that the older "*Viviparus*" of the literature really belong to the genus. The species *beaumontianus* still resembles the marine Turbinids, especially in the relatively clear cone-shape of nearly equal height and breadth (compare Fig. 1 with Fig. 2). From a form like this diverge: a "broad" series, in which the shells remain relatively broad, whilst the whorls become more inflated and the suture deeper, ending in the living species *Viv. viviparus*, which is widely distributed in Europe; and a "slender" series, whose representatives are more slender, retain more the flattened whorls, and already early resemble in some degree the recent species *Viv. pyramidalis*, in Northern Italy. From the slender series there descend: slender forms, whose whorls, however, become more inflated, leading to the recent species *Viv. fasciatus*; and the famous branching genealogical tree of the Pliocene Slavonian Paludines, consisting in direct lines of descendants.

The female genital apparatus of the three recent species named presents some differences, which, however, seem to correspond more to the different specific rate of propagation than to any phylogenetic

relation, the rate of propagation being greater, and the dimensions of the neonates smaller, in small and rapid streams than in larger bodies of water.

The numbers of chromosomes (*viv.* 7, *pyr.* 9, and *fasc.* 10 double-chromosomes in the stages of chromosome-conjugation)

FIG. 1. TURBO RUGOSUS. MEDITERRANEAN, RECENT. REPRESENTATIVE OF THE TURBINIDAE. ONE-HALF NATURAL SIZE

FIG. 2. VIVIPARUS BEAUMONTIANUS. UPPER CRETACEOUS DEPOSITS, ÉTAGE DE ROGNAC, SOUTHERN FRANCE. NATURAL SIZE

FIG. 3. VIVIPARUS VIVIPARUS VAR. AMPULLACEUS. UPPER PLIOCENE OF THE VAL D'ARNO (ITALY). NATURAL SIZE

would be in accord with the above phylogenetic seriation. In general, though with much variation from the trend, the inclination of the aperture (i.e. the mouth of the shell) in the phylogenetic evolution diminishes (compare Fig. 1 with Fig. 3). The primitive obliquity of the aperture of the marine Turbinids (Fig. 1), Trochids, Pleurotomariids and some fossil freshwater Viviparids (not even maximal in *beaumontianus*) is the same that results from rolling up a plastic cone to the shape of a snail-shell; it produces, in the animal creeping horizontally, a steep attitude of the shell. The "steep" aperture (Fig. 3), which in the creeping animal is more inclined to the horizontal, allows a shell to be turned more backwards (resulting in a horizontal situation of the spindle in highly evolved marine representatives of neighboring groups, e.g. *Conus*, *Murex*); in some fossils it is attained by the edge of the aperture being "drawn forward" (Fig. 3), which in recent forms is mostly equalized, the edge being plane again.

THE GENEALOGY OF THE PLIOCENE SLAVONIC VIVIPARUS

The genealogical tree of the Pliocene Slavonic *Viviparus* (*Paludina*) shown in Fig. 4 is considerably simpler than the classic sketch of Neumayr (1875), from which it differs especially in beginning with *leiostracus* (which already greatly resembles the recent *pyramidalis*; in the same way *grandis*, seen in Fig. 4, the Transylvanian fossil form, is a giant form of *leiostracus*, closely corresponding to the living Mantuan giant form ("*mantovana*") of *pyramidalis*), instead of *neumayri*. The latter is regarded as an already more inflated variant in the direction of *fasciatus* (in the same deposits, whilst the steps above *pannonicus* are stratigraphic and consequently chronologic). A great simplification is effected by the omission of some doubtful species and by uniting two (*dezmanianus* and *nothus*, the latter regarded as merely a modification caused perhaps by wave action). My arrangement differs also from Neumayr's in the separate derivation of some broader forms (not included in Fig. 4) from the above "broad" series and in the separation of

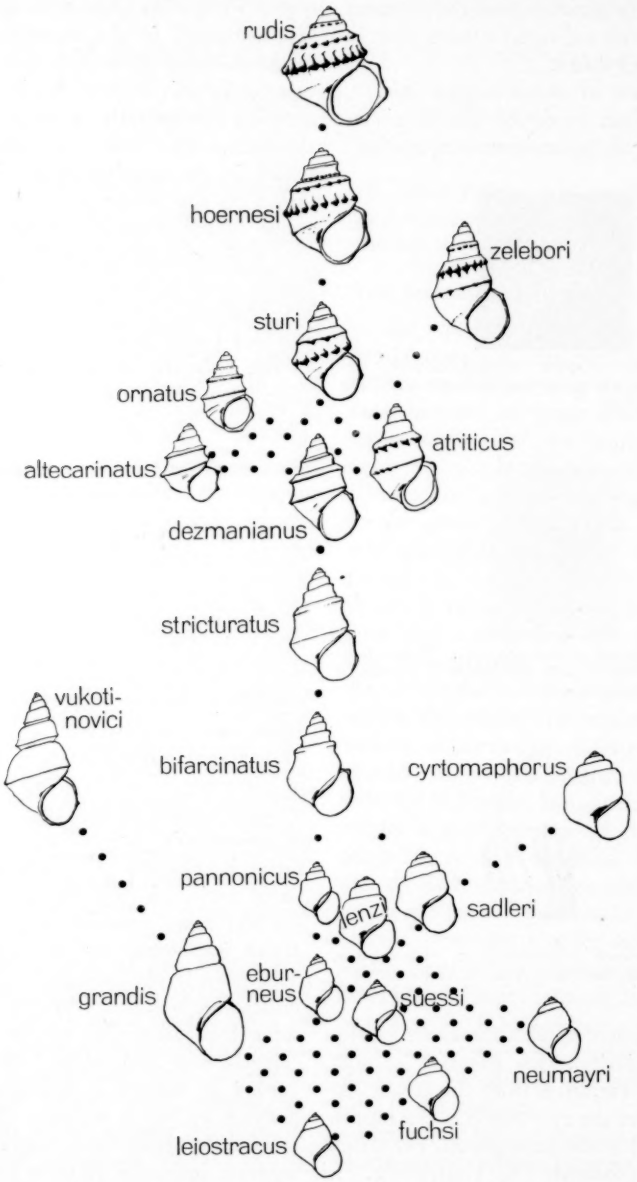

FIG. 4. GENEALOGICAL TREE OF THE PLIOCENE SLAVONIAN PALUDINES (VIVIPARUS)

the forms of the island Kos (apex very acute). The Slavonian snails clearly show the increasing "Tulotomoidy" (i.e., angularity and nodosity, convergence to the North American recent subgenus *Tulotoma* [in Alabama] of the genus *Viviparus*), increasing thickness of the shell, and embryonic similarity in the sense of K. E. v. Baer (or, in my terminology (1927), ontogenetically increasing deviation). The latter is not so broad as the less exact "biogenetic law" or "biogenetic rule"; the young of the descendant species resemble those of the ancestral species, especially in early stages of development. In the step *dezmanianus* → *sturi*, however, the new character, nodosity, appears already in the young; often it vanishes later, sometimes it persists; as a result of which there is a sudden appearance of the character in the series of the adults.

STATISTICAL METHODS

In order to characterize as objectively and distinctly as possible the various species or collections, the height (H), breadth (B) and weight (g) of each individual were determined. The first aim of these measurements is to give exact information upon the material instead of the too customary, merely subjective characterisations as "broad," "slender," "shell thick," etc., or instead of the determination merely of the range. For every form, for individuals of more than 10 mm. height, a linear equation between H and B has been fitted, for instance: *beaumontianus*, $B = 0.78\ H + 2.6$ mm.; *viviparus*, $B = 0.63\ H + 5.4$ mm., *pyramidalis*, $B = 0.55\ H + 5.2$ mm. Phylogenetically, on the whole the coefficient of H diminishes, and the constant term increases; in other words, the shell passes more and more from the cone-shape to the "tun"-shape (upper half of a tun), in which the older individuals are more slender in proportion to height than the younger. Ten individuals are a very good sample, from which an equation of high reliability for the respective locality can be calculated. What still needs correction, is not so much the fact that the complete curve, including the young of less than 10 mm. height, is probably a parabola, but the lack of a formula for the probable error of the equation; in practice, however, this is seldom employed by me and is not of great importance for my conclusions.

The simple calculation for finding this linear equation between B and H is as follows: n being the number of individuals at hand, we take the mean height H_1 and the mean breadth B_1 of the $\frac{n}{2}$ smallest individuals and similarly the mean height H_2 and the mean breadth B_2 of the $\frac{n}{2}$ largest.

Then

$$H_2 \frac{B_2 - B_1}{H_2 - H_1} = z;\quad B_2 - z = y;\quad \frac{B_2 - B_1}{H_2 - H_1} = x;$$

and

$$B = x \cdot H + y.$$

Several "forms," until now described under separate names and partly used for the construction of phylogenetical hypotheses, could convincingly be demonstrated by this calculation to be nothing more than the rare extremes of variation in breadth especially on the slender side, in consequence of old age, sometimes in connection with slow growth. The details of this, however, are of special interest only for the European zoologist. Furthermore, for each individual the weight-index $S = g \cdot 10^4 / (H \cdot B^2)$ is found and thence, with caution, the mean weight-index, both for the species as a whole and for the smaller (younger) and the larger individuals. Then, taking account of

the position and the number of winter-rings, in the recent species the local forms, mostly phaenotypic (somatic), are analyzed, for instance: a large form which, in growing, remains broad, has grown rapidly in youth; a slender giant form has grown slowly in youth; a stunted form is already slender in proportion to height (demonstrated by the measurements: slenderness of age). Such differences in average slenderness or breadth are scarcely recognizable by the eye, except by a very practiced one; and it is impossible to deal with them, except by measurement.

HYBRIDIZATION

Other chapters treat of hybrid populations after the demonstration of one such living in the southern part of the Lake of Garda as hybrids between the two species *pyramidalis* (shell thin, with bands) and *ater* (shell thick, black, perhaps a relatively new mutation from *pyramidalis*, also with nine double-chromosomes); in the hybrid population the shells are with bands, or black, or intermediate; the thickness and color of the shells varying independently. In the females with bands, the embryos are all with bands; in the intermediate and still more in the black females, black embryos appear by the side of those with bands (consequently bands are recessive, black dominant). All other hybrid populations of *Viviparus* treated of by me hitherto being merely hypothetical, I do not wish to deal further with this aspect of the European fauna. Under ideal conditions—i.e. when both parent species are mixed in equal number with each other, and when the environment of the hybrid population produces no somatic modification (as in the case in the southern part of the Lake of Garda)—we must expect the equation and the average weight-index of the hybrid population to be midway between the two parents, and the variation (or the probable individual deviation) of *H:B* in each *H*-group and of *S* to be greater than in the parents. The best numerical evidence of this was found in a form hitherto much discussed, *spurius* among the Pliocene Slavonians, by regarding it as a hybrid between *sadleri* and *bifarcinatus*.

All I have mentioned here, of course, are only the briefest hints. Now, as may be seen, the above investigations follow many lines, in part new. Owing to this, it is not easy to bring all of the results in relation to other similar works.

As to the morphometry, no similar attempt has been made before; and I can scarcely hope soon to find many successors. Indeed, I have worked four years upon my material, of which time a considerable part was devoted to the elaboration of methods of measurement and calculation. But a successor can use it in shorter time and will necessarily be led to it when he endeavors to deal with as many measurements as are sufficient in the descriptive sense for characterizing the dimensions of both younger and older individuals. But the morphometry as detailed above, of course, cannot be used with shells of a more complicated mode of growth, for example the laced, spindle-shaped shells of *Clausilia*, or of *Fusus* among the marine forms, in which the relation between *H* and *B* is by no means linear.

WORK OF OTHER AUTHORS

Concerning mutation and heredity, I only wish to say that recently (Schlesch, 1930) in the species *Viviparus fasciatus* there have also been found—only occasionally, it is true—individuals with dark color, highly comparable in this respect to *ater*, the variant of *pyramidalis*, probably caused by an external factor yet unknown, and certainly of the same he-

redity as in the Italian form. Concerning hybridization between different species, other investigations of myself (1929) and of my student Möller (1932) bring clearness also into the middle European forms of the *Anodonta*-mussels, a much discussed problem for about 50 years (Clessin, 1884), which is now illuminated by indubitably proving that there exist not one (as Clessin thought) but two species, *cygnea* and *piscinalis*, which in some localities live together without interbreeding, whilst in others they seem to form hybrids, to judge from the intergrading characters of many individuals between the two species.

The above work on *Viviparus* being regarded in the first place as a phylogenetical one, the question arises, what similar works here afforded similar results. The classical investigations of Neumayr (1875), which are often regarded as a most convincing test of phylogenetical evolution, and in this respect compared to Reichenow's elucidation of the Tertiary Steinheimian *Planorbis*, were already mentioned above. From Gottschick (1919) and Plate (1919) we know that in the latter (the planorbs) the chronological changes are only somatic, the water of higher temperature rendering the shells more and more conical, but that the change was always reversible, when the hot springs cooled. To my mind, the variations in the Slavonian *Viviparus* are to a great extent genotypic, since hybridization between different types is probable. Even now, however, we do not know the cause of this great mutability: was it the increasing salinity of the water (Forbes, 1847), was it the effect of waves, or did the water become more and more brackish and fresh, as supposed by Neumayr? Thus, many questions still remain open, but, in contrast with Dacqué, who regarded the whole genealogical tree of the Slavonian *Viviparus* as merely a construction upon paper, we could convincingly demonstrate its reality, except for some points of which Neumayr himself, even more exactly than generally is known, emphasized the doubtfulness.

As to other works upon land and freshwater molluscs, we must confess that they give as yet very little phylogenetical information upon most of the families, and that most questions are still at sixes and sevens. Nobody can positively say whether the Palaeozoic Anthracosiidae-mussels or the American Carboniferous *Palaeorbis*, *Archaeozonites*, *Dendropupa*, etc., are ancestors of the Mesozoic and Caenozoic *Unio*, *Planorbis*, *Zonites*, *Pupa*. The giant work of Sandberger (1870–1875) notes, as it seems to me, in the Jurassic period the first indubitable representatives of *genera* of today. Following his chronological account, we see clearly the forms becoming more like the recent ones, the younger they are in the history of the earth's surface, but each form in its locality and time appeared we know not from where, and it is impossible to draw phylogenetical lines even approximately from one to another. Moreover, the author ascribes so many European fossil forms as nearest relations to an American or Asiatic living species; in other words, he saw the phylogenetic and geographic connections highly complicated; certainly, however, this is very speculative, for in *Viviparus* we could not follow him and often saw him overlook the much nearer intraeuropean relations.

Only in the genus *Pupa* and the family of Pupidae have we a paper of O. Boettger devoted to a task similar to mine, describing and connecting a group of snails, definitely terrestrial, and narrowly circumscribed in space and time. The genus *Pupa* has existed, according to the author, since the Pliocene in the species *Pupa*

muscorum, since the Pleistocene in other species, and the most of the Oligocene species, driven southward by the Tertiary sea or by the glacial period, have their nearest living allies in Oceania, the West Indies and upon Atlantic islands. Whether the latter conclusions are right, must be decided in future.

In the Viviparids of the world, a great work of Prashad (1928) which appeared shortly before mine, seeks many phylogenetic connections, but none between different parts of the globe, except, hypothetically enough, for Cretaceous or earlier times, in which these snails came up from the sea into the rivers or lived at first a short time in the latter. The author assumes landbridges between the different continents, a hypothesis scarcely very acceptable to-day. In detail, many of his results are very evident, e.g. that the Viviparids with ridges and nodes, the "Tulotomoids" in my expression, in the different continents, as Asia, Europe (here the Pliocene Slavonians), North America (the *Tulotoma's* in Alabama), are only convergent (cf. Annandale, 1924). The European forms being somewhat briefly treated in the work of Prashad, I found still unsolved the problems, to answer which was the first purpose of my investigation.

We could enumerate only a small number of works on material similar to mine. Surely, the restriction and, nevertheless, completeness in the material is the sole way leading to results free from contradiction, and I believe that in the future each investigator of such material will tend to treat it from newer points of view and by means of exact methods, which was my aim.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

BEFORE THE DAWN.

By John Taine. The Williams & Wilkins Co., Baltimore. $2.00. 8 x 5¼; vii + 247; 1934.

John Taine is the pseudonym of E. T. Bell, Professor of Mathematics in the California Institute of Technology and author of *The Queen of the Sciences* and *Numerology*, which have been reviewed in our columns. In this very readable romance he develops the idea that light leaves permanent traces on the objects on which it falls, so that a suitable television apparatus might reproduce the events of past ages. The pageant of evolution which he presents is much more graphic than that to be found in textbooks of paleontology. However, his dinosaurs struck us as disconcertingly anthropomorphic.

GÉNÉTIQUE ET ÉVOLUTION. *Analyse de quelques études mathématiques sur la sélection naturelle. Actualités Scientifiques et Industrielles, 158. Exposés de Biométrie et de Statistique Biologique, III.*

By Ph. L'Héritier. Hermann et Cie, Paris. 14 francs. 10 x 6½; 43; 1934 (paper).

This is a brief but clear analysis of the work of R. A. Fisher and Sewall Wright giving a schema of a mechanism of evolution founded on mutation and selection.

GENETICS

WORKING DOGS. *An Attempt to Produce a Strain of German Shepherds which Combines Working Ability and Beauty of Conformation. By Elliott Humphrey and Lucien Warner. Johns Hopkins Press, Baltimore.* $3.50. 9 x 5⅞; xiv + 253; 1934.

In 1924 Mrs. Harrison Eustis began breeding and training German shepherd dogs for police and military work and as guides for the blind. This very interesting book describes the breeding methods used to produce dogs of superior intelligence, disposition and physique for the different functions for which they are to be trained. Of the temperamental qualities the most important is sensitivity. An oversensitive dog is practically valueless as a worker, while an undersensitive dog is more difficult to train than one of medium sensitivity. Intelligence is highly correlated with success in working. Several traits such as olfactory acuity and distrust, are advantageous in certain forms of work but not in others. Thus distrust is desirable for a liaison dog but detrimental in most other types. Dogs with well developed chests and flanks were found to be more resistant to disease than those with poor development. Sensitivity seems to be inherited in Mendelian fashion but the mode of inheritance of most other traits has not yet been worked out. That the breeding program has been successful, however, is shown by the fact that the rating of the

dogs for most of the desired qualities has shown an upward trend and that, while during the first two years only 16 per cent of the dogs produced completed the courses of instruction and went into service, during the last two years the proportion has increased to 94 per cent. We may, with Pearl in his foreword, look forward to the day when dogs will be bred "capable of performing tasks which have not yet even been thought of as coming within the range of possibilities."

PLANT CHIMAERAS AND GRAFT HYBRIDS. *By W. Neilson Jones. Methuen and Co., London.* 3s. 6d. net. $6\frac{1}{4}$ x $4\frac{1}{4}$; viii + 136; 1934.

Biologists will welcome this account of plant chimaeras, plants "built up of two or more genetically different components arranged in a pattern more or less stable during the life of the individual." Although the problem of their natural origin is still unsolved they can be produced by saddle grafting the scion of one species, *Solanum lycopersicum*, for instance, on the stock of another species, e.g. *S. nigrum*, and subsequently cutting the scion off just above the union. From the layer of callus tissue that forms, adventitious buds develop; sometimes the core of such a bud will be derived from one species and the skin from another. The shoot developing from such a bud has properties intermediate between those of the species involved, and since the relative amounts of tissue in the bud derived from the two species may vary the structure of the shoot is variable also. Many chimaeras are of horticultural importance and numerous workers have studied them on that account. There is another group of workers who have regarded chimaeras as a fruitful field for the study of experimental morphology and they have obtained important results. Professor Jones has prepared a well-organized and well-written account of the literature on the subject, and has provided it with an index and a bibliography.

A BIBLIOGRAPHY OF PLANT GENETICS. *U. S. Department of Agriculture Miscellaneous Publication No. 164. By Marjorie F. Warner, Martha A. Sherman, and Esther M. Colvin. U. S. Government Printing Office, Washington.* 50 cents. $9\frac{1}{4}$ x $5\frac{7}{8}$; 552; 1934 (paper).

GENERAL BIOLOGY

JAMES JOHNSTONE MEMORIAL VOLUME. *By twenty-three contributors. University Press of Liverpool.* 21 shillings net. $9\frac{5}{8}$ x 6; x + 348; 1934.

The greater proportion of the papers in this volume deal with the geophysical or the biochemical aspects of oceanography. F. J. Cole contributes a biography of James Johnstone, who occupied the Chair of Oceanography at Liverpool at the time of his death in 1932, and E. S. Russell has a synopsis of Johnstone's "The Essentials of Biology." There is a paper on the life history of the Asteroid genus *Luidia*, a review of work on the color changes of fish, a study of the movements of herring as deduced from the catches in weirs set on all sides of a large bay, a bionomical study on *Cardium edule*, two papers on helminthology, a report on the fauna of an artificial pond by the seashore, and a comparison of the seasonal fluctuation of the plankton in the region of Australia and in the Irish Sea. A. C. Redfield has an article on the organic derivatives in sea water, there is a note on the possible presence of enzymes in sea water, and there are longer papers on the distribution of oxygen and salt content in relation to tracing the movements of large masses of water by T. G. Thompson *et al.* and by Gerhard Schott. Wüst has a paper on bottom temperature, Helland-Hansen reports detailed oceanographic observations on the North Sea and the Norwegian Sea, and Jacobsen and Thomsen report a similar study of the Straits of Gibraltar. There are three papers dealing with tides, a statistical paper on curve fitting, and a physical paper in Italian on the penetration of light into water. Three papers are in German, one is in French. Bibliographies are appended to each paper.

SCOLT HEAD ISLAND. *The Story of its Origin: the Plant and Animal Life of the Dunes and Marshes.*

Edited by J. A. Steers. W. Heffer and Sons, Cambridge. 15 shillings net. 8½ x 5⅝; xvi + 234 + folding map; 1934.

Scolt Head is a low-lying island about four miles in length off the east coast of England in the county Norfolk, a large part of its area lying in the inter-tidal zone. It is still undergoing rapid physiographic change, the formation of dunes and shingle beaches and the filling of marshes go on simultaneously with severe wave erosion in other places. The Cambridge Geography School has established a laboratory there and has been making a careful and varied study of the island and its flora and fauna. Mr. Steers contributes a long section, profusely illustrated with old and new maps and with photographs, on the physiography of the island; V. J. Chapman has a long and excellent chapter on plant ecology, and Miss E. L. Turner has an interesting chapter on the birds that breed on the island. There are shorter papers on pollen analysis of peat, and on the ecology of mammals, invertebrates, bryophytes, and lichens. This represents first-class ecological research in all the departments of a well-rounded cooperative research project and except for the lack of an index there is no fault to find with the presentation of the results.

TRANSACTIONS OF THE BOSE RESEARCH INSTITUTE, CALCUTTA. *Vol. VIII*, 1932–1933. *Biological and Physical Researches.*

Edited by Sir Jagadis Chunder Bose. Longmans, Green and Co., New York and London. $8.40 (U. S. A.); 21 shillings net (Great Britain). 8¾ x 5½; vi + 266; 1934.

According to Western habits of scientific thought, to which Sir Jagadis Chunder Bose does not cater, the best paper in this volume is P. C. Basu's anthropometric study of 250 Munda men, a tribe of uncertain phylogenetic affinities living in the highlands of Central India. Except for stature, which averaged 1581 mm., all of his 15 measurements were made on the head or face. The usual indices and measures of variation are presented; for example, the cephalic index is 74 and the nasal index 83. There is a good, but brief, discussion of the non-quantitative characteristics usually studied by physical anthropologists, and an intensive craniometric study involving 64 measured characteristics and 31 indices made on 7 Munda skulls. Both sets of measurements were made with standard anthropometric technique. Also of possible interest to Occidental scientists are papers of the seasonal variation in manganese content of the leaves of conifers, on the chemical constitution and properties of substances isolated from Indian plants, and two papers on physics. These papers are provided with bibliographies and are presented in the conventional way.

In striking contrast, however, are seven papers by Bose and his associates of the type he has been publishing for about 30 years which involve elaborate automatic recording devices to magnify movement or elongation of plant organs, fish gills, or visceral organs, and to register their movements on smoked plates. Somehow the discussion is never very profound. There are no bibliographies, no indication as to the relation of the findings to the work of other people, no tables of data, and no definite information about variation or repetitions. There is no index.

L'ANALYSE MITOGÉNÉTIQUE SPECTRALE. *Actualités Scientifiques et Industrielles, 150. Exposés de Physiologie, IV.*

By A. and L. Gurwitsch. Hermann et Cie, Paris. 12 francs. 10 x 6½; 39; 1934 (paper).

Probably what most biologists want to know about this booklet is, what figures does Gurwitsch give for the intensity of mitogenetic radiation, and how do these figures compare with the sensitivity of the Geiger-Müller counter, the only physical means of detecting this radiation.

"An approximate calculation gives us the following values: we shall take as point of departure the intensity of 1000 quanta per second per square centimeter—according to the data of Rajewsky, Frank and Rodionoff."

The two most recent attempts (not noted in this brochure) to detect mitogenetic radiation, that of Gray and Ouellet with a counter sensitive to 50 quanta per second per square centimeter and that of Lorenz with a counter sensitive to 10–15 quanta per second per square centimeter, ended in failure; and in both cases the mistakes

made by previous workers, some of whom have found positive effects, were identified and avoided.

Gurwitsch discusses briefly the mitogenetic spectra emitted by solutions in which biochemically important reactions were taking place, the spectra being constructed from the growth responses of yeast exposed in a quartz spectroscope. This booklet is far below the high standards of the other numbers of the *Actualités Scientifiques*.

DYNAMIC BIOLOGY.

By Arthur O. Baker, Lewis H. Mills. Edited by William L. Connor. Drawings by Earl Wolf. Rand McNally and Co., New York. $1.72. $7\frac{7}{8}$ x $5\frac{3}{8}$; x + 722; 1933.

The apparent tendency in high school biology texts seems aimed to make it unnecessary for the teacher to use any initiative whatever. The idea may be good for classes inflicted with poor teachers but it does seem too bad to penalize the good teachers to quite the extent that such dramatizations of subject matter must. Far be it from us to advocate dry-as-dust texts—although to a biologist it does not seem as though any book could make general biology dull—but there is surely a limit to the jazzing up that is desirable.

There are many excellent features to this particular book. The amount of emphasis on ecology and the chapters on genetics and paleontology are especially good, although the genetics chapter seems rather detailed and complicated for high school students. The diagrams and drawings are excellent, but many of the photographs are poorly reproduced. One particularly good feature is the indication of pronunciation given for all technical terms. There is a classification table for both plants and animals and a glossary and index.

BIOLOGIE DER FORTPFLANZUNG IM TIERREICHE. *Verständliche Wissenschaft XXII. By Ulrich Gerhardt. Julius Springer, Berlin.* 4.80 marks. $7\frac{1}{8}$ x $4\frac{5}{8}$; viii + 149; 1934.

The present book on the biology of reproduction is the twenty-second of a popular science series. The present volume is designed to make the vast field of animal reproduction intelligible to those who are not specialists in the field. The book does not consider reproduction according to the systematic classification of animals, but discusses various phases of the morphology and development of sexual organs in general terms with examples taken from specific animals. There is only a very small amount of space devoted to asexual reproduction.

VITALITY.

By Boris Sokoloff. E. P. Dutton and Co., New York. $2.00. $7\frac{1}{2}$ x $5\frac{1}{8}$; 181; 1934.

The first part of this book is concerned with the vitality of man and animals, believed by the author to reside in the cortex of the suprarenal, "the gland of life." The hormone of this gland is also dramatically called "the hormone of vitality." The second part develops the thesis that vitality has as its most particular main source lactic acid. In fact the author becomes so eloquent over the merits of lactic acid as fuel for the brain, general internal antiseptic, and stimulator of vitality that the reader begins to wonder if all depressions and feelings of malaise could not be cured by a squirt of lactic acid. The third part is called "The crisis of vitality—cancer." There is an interesting chapter on Napoleon's case. The book suffers from its attempt to popularize too recent research in problems of vitality and cancer. When there is more definitive knowledge concerning these problems, and conclusions have been more thoroughly and widely established, then such a book for lay consumption would have more value.

ELEMENTS OF MODERN BIOLOGY.

By C. R. Plunkett. Henry Holt and Co., New York. $3.00. $8\frac{3}{8}$ x $5\frac{3}{8}$; viii + 540; 1934.

This is a text somewhat simpler but along the same general lines as the author's *Outlines of Modern Biology*, already noticed here (Volume 5, p. 364). Some of the more

difficult sections of the earlier text involving a student's knowledge of chemistry and physics have been omitted, while other parts have been expanded and further clarified. What has already been said about *Outlines of Modern Biology* applies to this book.

BIOLOGY FOR SCHOOLS. *A Textbook Suitable for School Certificate and Similar Examinations. Second Edition.*
By E. R. and A. V. Spratt. University Tutorial Press, Cambridge. 4s. 6d. 7¼ x 4¾; viii + 407; 1934.
An excellent, well-written textbook of Biology for beginners of high school age. The authors are not afraid of using big words, and there is no sugar coating as is so often the case in such books designed for the pre-college student. In fact any student started in on this book would probably be better acquainted with the fundamentals of biology than most are after a first year college course.

VIE ET SURVIE.
By Edgard-Emmanuel Bonnet. Messageries Hachette, Paris. 20 francs. 9 x 5½; 489; 1934 (paper).
Idealistic speculations on the origin of physical and spiritual life and its transmission. It lacks the fervor and dialectics of many works of its type but the author has some knowledge of scientific facts which he uses very adroitly for his metaphysical interpretations.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 429. Polarisationsoptische Analyse des submikroskopischen Baues von Zellen und Geweben.*
By W. J. Schmidt. Urban und Schwarzenberg, Berlin. 13.50 marks. 10 x 7; 231; 1934 (paper).
This number of the Abderhalden *Handbuch* series outlines the theory and technique of polarization analysis of the submicroscopic structure of plant and animal cells and tissues, with directions for preparing the various materials to be analyzed.

BERMUDA OCEANOGRAPHIC EXPEDITIONS 1929–1930. *Zoologica, Vol. 13, Nos. 1 and 2.*
By William Beebe. New York Zoological Society, New York. 75 cents net. 9½ x 6¾; 36; 1931 (paper).
BERMUDA OCEANOGRAPHIC EXPEDITIONS 1931. *Zoologica, Vol. 13, No. 3.*
By William Beebe. New York Zoological Society, New York. 25 cents net. 9½ x 6¾; 9; 1932 (paper).
A brief account of the establishment and present method of carrying out routine work in the Bermuda Oceanographic station, supplemented by a list of individual nets hauled in for 1929, 1930 and 1931, with accompanying data.

BIOLOGY. *Elementary Science Series.*
By E. R. and A. V. Spratt. University Tutorial Press, Cambridge. 1s. 9d. 7¼ x 4⅞; viii + 140; 1934.
Designed for school children, and on the whole better than most such books, as it is more accurate and thorough.

BULLETIN DE L'ASSOCIATION DES DIPLÔMÉS DE MICROBIOLOGIE DE LA FACULTÉ DE PHARMACIE DE NANCY, *No. 8.*
9⅝ x 6¼; 36; 1934 (paper).

HUMAN BIOLOGY

REVELATIONS OF A PRISON DOCTOR.
By Louis Berg. Minton, Balch and Co., New York. $2.50. 8⅛ x 5⅜; vii + 255; 1934.
The psychopathology of prison inmates, the horrid ravages made by their drug addictions, their homosexuality, their venereal diseases, their "rackets" and riots, all set forth in great detail in this book by Dr. Berg, who has been Senior Medical Officer on Welfare Island, make depressing reading. But the author is hopeful.

Most offenders can and must be reclaimed. To accomplish this we must reorganize our legal system. Equality before the law for rich and poor, quick trials for all and uniformity of sentence for similar offenses, are imperative. It is the knowledge that there is no immunity from arrest, no possibility of police or judicial corruption, and that impartial justice will follow apprehension, that accounts for the difference between our enormous crime rate and England's modest one.

No court in the land should be without its psychiatric adviser; no sentence should be pronounced without the aid of individual recommendation from a competent medical examiner as to its length and nature, based upon study of the offender. In the last analysis, such a procedure would be able to secure adjustment in every instance through supervised probation, whereas all hope would be lost once the individual were confined even in the most ideal prison.

THE ANDAMAN ISLANDERS.

By A. R. Radcliffe-Brown. The Macmillan Co., New York; University Press, Cambridge. $10.00. $8\frac{3}{4}$ x $5\frac{1}{2}$; xiv + 510 + 19 plates and 2 maps; 1933.

Professor Radcliffe-Brown spent the years 1906 to 1908 in the Andaman Islands collecting the material upon which this book is based. It is much more complete and thorough, and naturally more modern in its methodology, than the study of the same people by Man (cf. QUARTERLY REVIEW OF BIOLOGY, Vol. 8, p. 113) a quarter of a century earlier. But it is interesting and valuable to have the two independent accounts for comparison. The material is presented under four heads: social organization, ceremonial customs, religious and magical beliefs, and myths and legends. Then follow two long chapters giving the author's interpretation of the "meaning" and "function" of Andamanese customs, beliefs, ceremonies, myths and legends. Methodologically these chapters are the book's most important contribution. Appendices deal with the technical culture and language. The book is well illustrated and indexed.

THE METHOD AND THEORY OF ETHNOLOGY. *An Essay in Criticism.*

By Paul Radin. McGraw-Hill Book Co., New York. $2.50. $7\frac{3}{8}$ x 5; xv + 278; 1934.

This vigorously written book will be extremely useful to beginning students of anthropology and human biology and will entertain older hands. This usefulness will be in no serious way impaired by the fact that the author is an advocate of one particular view as to the philosophy of ethnological methodology, for he plays fair in his exposition of the views he opposes. Ethnology is the study of aboriginal cultures. Anthropologists divide into three camps in their attitudes toward primitive cultures, and these attitudes reflect themselves in methodology, according to Radin. One attitude conceives the purpose of ethnology to be to trace the evolution of culture; another to demonstrate the diversity of cultures; the third, merely to describe objectively with no purpose other than description. Radin is a forthright but good-tempered critic. We think he does his case for the purely objective descriptive attitude much harm by his insistence (unnecessary and not altogether well-informed as it seems to us) that ethnology has no affinities with the natural or biological sciences.

The book is well documented and indexed.

DIE TRÄGER DER KULTUR.

By Walter Scheidt. Alfred Metzner, Berlin. 4.50 marks. $8\frac{5}{8}$ x $5\frac{1}{2}$; 131; 1934.

This book embodies the content of a lecture course on eugenics given for a number of years at the University of Hamburg. Its approach differs somewhat from that of the conventional English and American treatises on eugenics. The nucleus of the argument is the national culture of the German people, and what the author discusses are the biological factors that condition it, and in a statistical sense determine it. The general conclusion reached is pessimistic. In the 70 years from 1930 to 2000 the author predicts that the combined percentage in the population of the highly gifted, those above the average, and those of average gifts, will decline from 67 percent to 47 percent, and the proportion of inferior folk correspondingly increase. The book has no index and few bibliographic citations.

HISTORY OF PALESTINE. *The Last Two Thousand Years.*

By Jacob de Haas. The Macmillan Co., New York. $3.50. 8½ x 5¾; xxvii + 523; 1934.

In the introduction of this book the author says:

> The history of the country, as a whole, and of particular places, has been one of alternating violent or gradual change. Mutation, in all things, has been the keynote of Palestinean history these two thousand years. It could not well be otherwise, for no other land has been so forced to obey the whim of conqueror; or has been the meeting place of so many diverse races and peoples.

Three world religions have been born here and a fourth, that of the Druzes, persisted for a thousand years. In spite of the wars that repeatedly swept over the country from the time of the Roman conquest in the year 70 up to the advent of the Turk the country long remained enormously rich in its agricultural products. Its centers of population had a high mobility induced by the ever changing political, social and economic conditions. By the middle of the thirteenth century the disintegration of Palestine had commenced. A subjugated land, misruled by its masters, its forests destroyed by invaders, its people crushed by plague and epidemic, it gradually became more like the desert waste around it. Its cities fell into decay and its rural regions became desolate. For five hundred years this decay continued. From the time of the discovery of America, Palestine became an almost forgotten country. With a few notable exceptions the buildings of present day Palestine are less than three centuries old. The author of this volume has traced with meticulous care the important events of Palestinian history. Written without bias the student will find it a useful reference book. The general reader will find it absorbingly interesting. The chapters are documented and there is a detailed index.

THE TWILIGHT OF PARENTHOOD.

By Enid Charles. W. W. Norton and Co., New York. $2.50. 7¾ x 5⅜; vii + 226; 1934.

Dr. Charles belongs to the newer school of writers on population who view with alarm, not the prospect of overpopulation, as did the followers of Malthus, but rather that of population decline. As Dublin and Lotka have pointed out, the decline of the birth rate has resulted in an excess of women of the child bearing ages, so that even if the decline in the birth rates at ages should cease, the crude birth rate would continue to decrease until a stable age distribution was reached. In this way a population which is actually increasing at the present time may be potentially stationary or even decreasing, and Kuczynski has found that a number of European countries are already in this potentially decreasing state. Incidentally, in her exposition of the newer methods of demographic statistics Dr. Charles gives rather the impression that these are due almost entirely to Kuczynski. Actually the net reproduction rate was first used by Boeckh, while the development of the mathematical analysis of the dynamics of population is mainly due to Lotka.

In the discussion of whether the observed decline in the birth rate is the result of increase in density of population, as Pearl has concluded, or of some special cause such as the spread of contraception, it is scarcely correct to say that "Pearl himself was unable to offer any explanation of the fall in fertility observed in *Drosophila*." The latter has found evidence "that crowding produces the observed effect on rate of egg laying primarily, though probably not solely, as a result of a collision or interference action of the flies upon each other, which alters the normal physiological equilibrium and processes of the individual. . . . . " Nor is the inverse relation between density and fertility confined to *Drosophila*. It has also been observed in the flour beetle, *Tribolium confusum*, through most of the density range, in fowls and in human populations.

BENJAMIN RUSH, PHYSICIAN AND CITIZEN, 1746–1813.

By Nathan G. Goodman. University of Pennsylvania Press, Philadelphia. $4.00. 9 x 5⅞; 421; 1934.

It is unfortunate that this first full biography of Benjamin Rush is not always well presented. The author, however, has been tireless in his research and has accumulated a large amount of authentic material concerning this great physician, patriot and reformer. In so brief a review it is possible to indicate only a few of Rush's many interests. He did not confine his attention solely to medicine, although in this field he was a pioneer along many lines. One of the first advocates of preventive medicine, the first American psychiatrist and the first formal professor of chemistry, the founder of the free dispensary in Philadelphia and of the College of Physicians, he still found time faithfully to attend to his extensive practice and to write numerous treatises on a wide variety of topics. Both his book on mental disease (a classic for 50 years) and his chemistry were the first of their kind to be produced in this country. His interest in social reform led him to found the first temperance and anti-slavery societies, the first Sunday school system, and Dickinson College. A signer of the Declaration of Independence, his patriotism was intense and if during the Revolutionary period he made many bitter enemies no one ever accused him of selfish motives. All students of medicine and public health will find this an absorbing book but it will be equally interesting to the general reader who will find in Benjamin Rush another of those great figures who helped to mould the destiny of our country. The volume contains a few illustrations, collections of notes, a lengthy bibliography and an index.

MEDICINE MAN IN CHINA.

By A. Gervais. Translated from the French by Vincent Sheean. Frederick A. Stokes Co., New York. $2.75. $8\frac{1}{8}$ x $5\frac{1}{2}$; 336; 1934.

Dr. Gervais, a French physician, gives an intimate portrait of China, particularly around Chengtu in the western part of the country. His attempts to practise medicine in the European manner and the uselessness of combatting dirt and disease in a race that lives apparently unconscious of the former and resigned to the latter are well portrayed. The following are examples of what the physician is obliged to cope with: "Have you any fever?" "Yes, in the palm of my left hand." To a woman: "What is troubling you?" "I lost my son last year and I've caught the sickness of sadness. Give me a remedy." To another: "What are your pains?" "I am not ill. I only want to know if I am strong enough to take a bath."

When a class in dissection was started, the townspeople mobbed the classroom. The Chinese governor, eager to promote the cause of medical education, proposed that the next dissection should be performed upon a live criminal. To dissect a cadaver was to profane the dead; to dissect a living subject was merely a new and ingenious mode of execution. Unfortunately, though this solution satisfied the Chinese mores, it did not satisfy Dr. Gervais' European mores.

The author gives many vivid examples of the vast differences between the Chinese and Western ideas of law, honesty, cleanliness, sickness, marriage and death. From these we receive a feeling of futility in even attempting to change a race so different in background and so utterly absorbed in past tradition. We begin to realize that it is not a matter of months and years but of generation upon generation before Western ideas of progress are even partially understood.

SPARKS BENEATH THE ASHES. *Experiences of a London Probation Officer.*

By Mary Ellison. John Murray, London. 6 shillings. $7\frac{3}{8}$ x $4\frac{7}{8}$; xvi + 240; 1934.

A book that all those interested in social welfare should not fail to read. It recounts the experience of a probation officer in the slums of London. Her case histories are most interesting. But even more interesting to the reader will be what this book quite unconsciously reveals of the author herself. Probably comparatively few social workers have the wisdom, discernment, and humor that Mrs. Ellison has. In her preface the writer (Mary Stopford before her recent marriage) says:

Some maintain that the balance has swung too far in favour of the individual in England to-day and that sentimentality is ruining the administration of justice. This is sometimes true. The actual selection of the individual may be wrong. It is unwise to force probation on one who does not wish for it, as, for example, on a prostitute unwilling to abandon her mode of life. To do so is unfair to the Act, to the Probation Officer and to the woman herself.

Mrs. Ellison's office was her home in a basement flat in Pimlico and at all times the door was open. This she believes is essential to successful welfare work. Troubles cannot always wait for the office door to open at ten o'clock in the morning. ". . . immediate action at the psychological moment may turn the complete tragedy of to-morrow into the successful start of a new life." The various chapter headings of the volume are as follows: A day's work; Life in the slums; Stray sheep; Gangs, gangsters and thieves; Family differences; Queer people and dear people; Drunkards, drug addicts, suicides; Women of the streets—the broken-hearted. The volume is not indexed.

RICHARD TREVITHICK, *the Engineer and the Man.*

By H. W. Dickinson and Arthur Titley. University Press, Cambridge; Macmillan Co., New York. $5.50. 9½ x 6⅛; xvii + 290 + 18 plates + folding pedigree chart; 1934.

Richard Trevithick is one of the great engineers of all times. Possessing a brilliant but erratic mind he had little theoretical knowledge upon which to base his inventions. His ideas came to him with the rapidity of intuition. No sooner were they conceived than were they put into execution with lightning-like speed. Watt was the inductive philosopher developing his low pressure theories with slow and meticulous care. About 20 years after he had introduced his engine into Cornwall Trevithick, still under 30, developed almost over night his high pressure steam engine, the forerunner of our boilers and turbines of today. It is unfortunate that so little is known of the eleven years that the inventor spent in South America, where he went to install his engines in the great silver mines of Peru.

The authors have based their book on the two large but somewhat obscure volumes which Trevithick's son Francis produced some 60 years ago, adding new material that has come into their possession. They have made an extremely interesting book both for the general reader and for the engineer. The volume is abundantly illustrated with reproductions of Trevithick's drawings, contains a list of the inventor's patents for inventions, a pedigree of his family, a bibliography and an index. It has been issued as a memorial volume on the centenary of the death of the great engineer.

TIMBUCTOO.

By Leland Hall. The Cresset Press, London. 8s. 6d. net. 8½ x 5⅜; xiii + 278; 1934.

SALAH AND HIS AMERICAN.

By Leland Hall. Alfred A. Knopf, New York. $2.00. 7½ x 5; 199; 1934.

Both of these books are entertaining. *Timbuctoo* reveals much of the native life and customs of the French Sudan. *Salah and his American* centers around one person, the negro lad (a former slave) who attached himself to the author in Casablanca and made himself part of the author's life for a brief period. At the time of parting Salah was provided with a way of making his living but Mr. Hall had many doubts of the wisdom of this which meant for the gentle and honest Salah battling with dishonest and unscrupulous people and the ultimate breaking down of his fine character. In slavery "Salah's chances for what we call happiness—chances which are seldom for us to fight over or relinquish—would be favorable."

In Timbuctoo which is south of Morocco on the opposite edge of the Sahara desert the author established a home for himself, acquired servants and mingled with the natives. He writes of the many friends that he made; the return of the great salt caravan when over a thousand Arabs and their camels poured into Timbuctoo after several months in the desert; of the ancient university and mosques; of the Songhai who trained in literary Arabic and French maintain their ancient tradi-

tion and exhibit a "notable elegance of manner." He does not mention, however, Père Yakouba, the "white monk" of Timbuctoo, and the reader naturally wonders why not? The very few illustrations in the books are sufficient since Mr. Hall's word pictures are vivid and colorful. Neither volume is indexed.

EARNINGS AND STANDARD OF LIVING OF 1,000 RAILWAY EMPLOYEES DURING THE DEPRESSION. *U. S. Department of Labor. By Carter Goodrich. U. S. Government Printing Office, Washington.* 10 cents. $9\frac{1}{8}$ x $5\frac{7}{8}$; vi + 56 + 2 plates; 1934 (paper).

This pamphlet, unlike the majority of reports dealing with the recent economic depression, has to do, not with the unemployed, but with a group of workers who still held their jobs through the worst months of 1933. Such a group is a highly selected one but represents a large and very important class of workers whose reactions to the depression are but little known. The survey shows that the depression brought to these railroad men and their families a much greater reduction in net income than is generally appreciated. Taking account of all available sources of income only one quarter of them received in 1932, as much as $1,750 per year; nearly 60 per cent received less than $1,500. Study of the attempts of these families to manage their financial affairs revealed that few had cut down on their obligations. Many gave generously to needier families; more than a fifth took less fortunate relatives or friends into their own homes. Only 72 (out of the 1,000) received aid from public or private relief agencies. Attempts to economize include the abandonment of educational opportunities, large reductions in expenditures for food and clothing, almost complete curtailment of even the most inexpensive forms of recreation, and dangerous neglect of health needs. Despite these economies, the cash savings of most of the families were completely exhausted, many had lost their homes, half of them report sacrifice of insurance policies, and nearly 60 per cent had gone seriously into debt.

REBEL DESTINY. *Among the Bush Negroes of Dutch Guiana. By Melville J. and Frances S. Herskovits. Whittlesey House, McGraw-Hill Book Co., New York.* $3.00. 9 x $5\frac{3}{4}$; xvii + 366 + 15 plates; 1934.

More than a century and a half ago slaves imported into Dutch Guiana revolted and escaped to the bush which lies to the north of the Amazon basin, where they established a "Little Africa." Protected from molestation by the whites by treacherous rivers and the dense jungles they increased in numbers and in course of time were given their freedom by the Dutch. Of the three tribes which then became free the Saramacca has had the least contact with outside influences and has preserved to a marked degree tribal customs and beliefs which their ancestors brought with them from Africa. It is this tribe with which the present volume deals. In their treatise the authors have stressed the "Bush Negro's attitudes towards his own civilization and his own logic in explaining his customs." It is an absorbing book which the general reader will do well to include in his reading list. The illustrations are well chosen, those displaying the artistry of the tribe being particularly interesting. Included in the volume is a section on glossary and linguistic notes and an index. The scientific discussion of the ethnological data and the comparison of the Bush Negro with other negro groups in the New World have been reserved by the authors for other publication. The completed study forms part of a general investigation which the authors are making on the physical and cultural characteristics of the negro of the New World.

AN INTRODUCTION TO PARETO, HIS SOCIOLOGY. *By George C. Homans and Charles P. Curtis, Jr. Alfred A. Knopf, New York.* $2.50. $7\frac{1}{2}$ x 5; xiii + 299 + vi; 1934.

The authors are to be complimented for their courage in attempting to "popularize" the Sociology of Vilfredo Pareto. Except for some changes in nomenclature and a substitution of illustrative examples

they have remained faithful to the original. "Residues," "Derivations," etc. are very clearly defined. It is no mean task to summarize intelligibly Pareto's monumental work in the brief space used by the authors and whatever weakness there results should be condoned. We dislike, though, the repeated assertions of the mathematical difficulties encountered in the original. Actually, except in rare instances, Pareto makes use of procedures familiar to most college students.

As Pareto repeatedly stated, the authors have emphasized that in the analysis of "teorie non-logicosperimentali" by means of "Residues" and "Derivations," the various categories of these are only tentative; the same is to be said for their application to the study of the movement of social classes. This should serve as a spur to a revision, reclassification and extension of the categories and method by serious students of social sciences and human biology not hampered by prejudices, political, ethical, or religious. It is to be hoped that this book will serve such a purpose.

THE PRAIRIE PROVINCE OF ILLINOIS. *A Study of Human Adjustment to the Natural Environment. Illinois Studies in the Social Sciences, Vol. 19, No. 3.*

By Edith M. Poggi. University of Illinois Press, Urbana. $1.00. 10½ x 7; 124; 1934 (paper).

An interesting study in human adjustment to natural environment which the investigator has worked out with considerable detail. The survey includes numerous maps and tables, a lengthy literature list and an index.

This study represents an attempt to discern the character and influence of the various elements of the natural environment—topography, soil, climate, vegetation, mineral resources, and location—upon the settlement and development of the prairie province of east-central Illinois, and to determine the extent of man's adjustment to these environmental conditions. Following the introductory chapter on the geographic regions of Illinois, the first part of the study consists of five chapters on the physical setting of the prairie province; the second part deals with agriculture and mineral industries as major human adjustments; and the third part is an interpretation of the geographic and economic conditions influencing settlement and development.

WHAT ABOUT ALCOHOL? *An Illustrated Outline of Scientific Facts about Alcohol and Alcohol Drinking.*

By Emil Bogen and Lehmann W. S. Hisey. Scientific Education Publishers, Los Angeles. $1.50. 9¾ x 6⅝; ix + 112; 1934.

The conclusions of this volume, all of which, according to the authors (with whom we cannot whole-heartedly agree on the point) have been proven true, are as follows:

Alcohol is a clear liquid formed by fermentation of vegetable matter. It is quickly absorbed but slowly burned up in the body. It cannot build or repair the tissues. It makes the drinker feel warm, but really lowers his temperature. It weakens muscular control and makes the drinker tire more quickly. It dulls the senses and depresses the mind, causing loss of self-control. It is not a good medicine for many sicknesses for which it has been used. It may, instead, cause many sicknesses and make other sicknesses worse. Large amounts of alcohol cause drunkenness, but even moderate drinking has its dangers. The use of alcohol causes much expense and loss to the entire community.

Despite the fact that the authors claim to be presenting facts only in the book this reviewer entertains an ignoble feeling that the book is really motivated by the reformers' spirit and is, in effect, intended to be propaganda against alcoholic imbibition. The illustrations are supposed to provoke laughter: the reviewer was antagonized by them.

VIE ET RAJEUNISSEMENT. *Une Nouvelle Méthode Générale de Traitement et Mes Expériences de Rajeunissement de Bologne et de Paris.*

By Francesco Cavazzi. Gaston Doin et Cie, Paris. 22 francs. 10 x 6⅞; xii + 73 + 17 folding plates; 1934 (paper).

This monograph consists essentially of two papers read before the Société de Médecine de Paris reporting the results of experiments on rejuvenation. The procedure, derived from an idea of Brown-Séquard, is that of repeated subcutaneous injections of "efferent testicular blood" taken from young and healthy horses. The experimental subjects were two groups of aged men, respectively of Bologna and Paris. The results were, so it is said, a return of vigor and strength, physical and spiritual. These effects the

author attributes to a testicular hormone which he is able to obtain at its source.

Not content with the exposition of such amazing results the author feels the necessity of introducing at every available point remarks of a personal nature, to tell the story of his failure in obtaining recognition in Bologna and to praise the somewhat better reception of the French. This effort to obtain sympathy for himself detracts much from whatever scientific value is to be attached to the results.

There is a laudatory preface by Ch. Richet and several very guarded testimonials by well known French physicians and physiologists.

THE RAINBOW BRIDGE. *A Study of Paganism.*

By John S. Newberry. Houghton Mifflin Co., Boston. $3.75. 8⅝ x 6; xv + 346; 1934.

This tale "of beasts and men and demigods and gods traces the history of paganism from the Stone Age to the Age of Perikles." The author has undertaken to

analyze the ideas that formed the basis of the religious cults of the cavemen, the Sumerians, the Chinese and Japanese, the Hindus, the Egyptians, the Persians, the Hebrews, the Phrygians, and the Greeks, and to co-ordinate these different racial attempts to exploit the supernatural, thus showing how the beliefs of the savage evolved into the creed of the most enlightened race of ancient times, and to establish the relation between the religious impulse and the rise of literature.

It is an interesting book that the author has given us. If at times he seems to be building upon insufficient evidence, at least the reader will acknowledge that he has done his best with available material. His work shows evidence of wide research and a painstaking accumulation of facts. Extensive notes are grouped together by chapter headings at the end of the volume and there is an index.

CHARLES W. ABEL OF KWATO. *Forty Years in Dark Papua.*

By Russell W. Abel. Fleming H. Revell Co., New York. $2.00. 8 x 5⅜; 255; 1934.

This biography, written by one of his sons, is the story of Abel's efforts to convert, with considerable success, the Papuan cannibals into Christians. The first part of the book, concerning the setting up and early years of the mission is the more interesting, interspersed as it is with bits such as the following:

"The true food for man!' old cannibals still avow—and they add that only of human flesh can one eat to excess without unpleasant after effects. Nevertheless, the people of this eastern part of New Guinea did not eat the flesh of their enemies either for pleasure or merely for a change of diet. The feast was a religious ceremony, expressing revenge and absolving them of a duty to their wronged dead. Those who partook thereby vindicated their reputation and disgraced the tribal kindred of those who were eaten. The spirits played their part in cannibalism, as in all else in Papuan life.

The latter part is concerned too much with the efforts to raise funds for the mission and the establishment of industrial enterprises. The book, however, gives a good picture of Abel's amazing energy, sense of humor, and a broadmindedness not usually associated with missionaries. Before teaching the natives Christianity he taught them cricket.

LAW AND ORDER IN POLYNESIA. *A Study of Primitive Legal Institutions.*

By H. Ian Hogbin. Harcourt Brace and Co., New York. $5.00. 8½ x 5⅜; lxxii + 296 + 8 plates; 1934.

Since most primitive tribes have no such differentiated legal institutions as judges and policemen many anthropologists have been led to the conclusion that these tribes have no law or at most only criminal law. According to these writers the savage is still too dumb to even think of breaking the customs of his tribe. Malinowski, however, in his more intimate first hand study of the Trobriand Islanders found a more complex mechanism, which is confirmed by his pupil Hogbin for the Polynesians of Ontong Java. The people of these tribes "keep to what custom—or, more correctly, law—bids them to do because they know that not far ahead there looms the occasion when in the name of the same law they will be entitled to demand the counter-service." If a wife

refuses to cook and tend her taro garden her husband will refuse to supply her with fish and vice versa. The spirits of the dead are also supposed to punish infractions of obligation. Moreover the injured party may hire a sorcerer to work his spells on the offender. Thus, although no courts enforce private obligations, there are advantages to those who fulfill their customary duties and corresponding disadvantages for those who do not.

HABITAT, ECONOMY AND SOCIETY: *A Geographical Introduction to Ethnology.*

By C. Daryll Forde. Methuen and Co., London. 15 shillings net. $8\frac{1}{2}$ x $5\frac{3}{8}$; xiv + 500; 1934.

By the simple expedient of an ordered and clear description of the economic, social and religious customs of "primitive" peoples (Bushmen, Eskimos, Boroes, Samoans, Kazaks, etc.) the author definitely reaffirms what, though well-established, is not always admitted; i.e., that physical environment is not the only factor in determining the type of economic civilization. In the first three chapters, each dedicated respectively to food gatherers, cultivators, and pastoral peoples, one observes peoples of different economics in the same environment and *vice versa*. A fourth chapter synthesizes the preceding and reviews the different economics with regard to particular historical and geographic background. The final conclusion is, as has been in part mentioned, that economic, social, geographic conditions are so intimately interrelated that we cannot speak of one as being the cause or effect of the others. A well written book with an extensive bibliography and very appropriate for students of ethnology.

THE PROBLEM OF THE AUSTRALIAN ABORIGINAL.

By E. R. B. Gribble. Angus and Robertson, Sydney. 5 shillings. $7\frac{1}{4}$ x $4\frac{5}{8}$; xv + 157; 1932.

In order to save the still-existing aboriginal tribes of Australia from the fate of the Tasmanians, or worse, the Reverend Gribble advocates their segregation on reservations similar to those for the Indians of this country. He furthermore recommends that their teaching be put in the hands of Christian missions rather than Government stations in order that the inculcation of christian ethics may counteract the vices they may have learned from the whites.

The book contains a deal of information, which may interest the anthropologist, concerning those tribes with which the author worked. There is also an unpleasant chapter on "Our treatment of the race," and one on the history of missionary efforts. We like this sentence concerning the Lutheran Society of Dresden.

"They laboured with much patience and great zeal, but after some years of toil and self-denial, abandoned the work among the natives, and undertook work amongst the white settlers."

THE RISE AND FALL OF THE CHOCTAW REPUBLIC.

By Angie Debo. University of Oklahoma Press, Norman. $3.50. 9 x 6; xvii + 314 + 26 plates; 1934.

The aboriginal Choctaws were a mild, quiet and kindly people. Being practical minded and adaptable they readily acquired the customs of the more advanced peoples with which they came in contact. The history of their race, and particularly of their relations with the United States Government is an exceedingly interesting one, but not one that the white race can be especially proud of. Land-hungry settlers assisted by the government devised every means possible to force the Indian race out of their fertile lands in the Mississippi regions to the more remote and supposedly less valuable lands further to the northwest. From the Civil War to the close of the century there was one continuous struggle of the Choctaw race to maintain its institutions and autonomous government. Miss Debo tells the story in great detail and has documented all of her points. The volume contains a number of maps and photographic reproductions, a lengthy bibliography, and is well indexed. The study is the sixth in the *Civilization of the American Indian*

series published by the University of Oklahoma Press.

HISTORY OF ANTHROPOLOGY. *The Thinker's Library, No. 42.*

By Alfred C. Haddon. Watts and Co., London. 1 shilling net. $6\frac{3}{8}$ x 4; xiv + 146; 1934.

This little volume, No. 42 of the Thinker's Library (British), can scarcely be considered a second edition of the author's first *History of Anthropology*, since it is made up of practically new matter. For its size it contains a great deal of interesting material. The author points out that more attention has been given to armchair workers than to field workers since he is dealing chiefly with "generalizations which proceed mainly from arm chairs." The three main sections of the book are human biology, cultural anthropology or ethnology, and comparative sociology. The literature cited is not detailed but sufficient for the student. There are a number of illustrations, and an author's index but no general index.

ERBLEHRE UND RASSENHYGIENE IM VÖLKISCHEN STAAT.

Edited by Ernst Rüdin. J. F. Lehmann, Munich. 14 marks (paper); 16 marks (cloth). $9\frac{7}{8}$ x $6\frac{3}{4}$; viii + 385; 1934.

The results of a symposium on mental and race hygiene held in Munich, January 1934, are set forth in 22 articles by 19 authors, on genetics, race origins, eugenics, and sterilization problems. The first article by the Bavarian Minister of Interior, concerning the value of race-hygiene for the state, is highly political. In fact there is hardly one of the articles which does not mention Hitler once or twice. There are two extra good chapters, however—one on the hereditary basis for race hygiene, incidentally written by a botanist; and the chapter on race origins written by Mollison, the latter being politically less biassed than any of the other authors. There is however an unfortunate tendency throughout the book to portray scientific facts chiefly in their relation to the present German political beliefs.

CENSUS OF 1930 IN NETHERLANDS-INDIA. *Volume II. Native Population in Middle-Java and the Native States of Java. Volume III. Native Population in East-Java.*

Census Office, 11 Schoolweg, Batavia-Centrum, Java, Netherlands-India. Vol. II, f. 8, Vol. III, f. 6. $13\frac{1}{2}$ x $9\frac{5}{8}$; Vol. II, xx + 256 + folding map; Vol. III, xvii + 222 + folding map; 1934 (paper).

The census official in Java has certain difficulties which do not trouble his brother in the Occident. Thus so few of the Javanese know their exact age that the population has been tabulated in three age classes: (1) infants not yet able to walk, (2) other non-adults, (3) adults. The boundary between classes 1 and 2 was easy to determine but that between classes 2 and 3 presented more difficulty. The criterion adopted was that a girl was adult when she was marriageable and a boy when he was physically able to go to work. However, in districts where it is the custom for girls to be married before puberty the enumerators, even though instructed that not all married girls need be adult, tended to disregard this instruction.

Another item with which Occidental census officials do not have to deal was number of simultaneous or concurrent wives. It was found that only 2 per cent of the married men had more than one wife at the same time.

A CONTRIBUTION TO THE ARCHÆOLOGY OF NORTH-EAST GREENLAND. *Skrifter om Svalbard og Ishavet*, Nr. 63. *Det Kongelige Departement for Handel, Sjøfart, Industri, Håndverk og Fiskeri. Norges Svalbard- og Ishaus-Undersøkelser.*

By Søren Richter. Kommisjon Hos Jacob Dybwad, Oslo. Kr. 25. $10\frac{1}{2}$ x $8\frac{1}{2}$; 149; 1934 (paper).

During 1929–31 the author was a member of the Norwegian Hunting Expedition in

North-East Greenland, and in the summers of 1932 and 1933 covered the same terrain with the Norwegian Greenland Expedition. In this work he tells about his explorations, beginning with a description of the country and continuing with his "finds"—remains of settlement and artefacts of various periods; hunting requisites, tools, household utensils, etc. Due to the sparsity of settlements found, and the small size of these, he concludes that this region never had a large Eskimo population. The treatise is profusely illustrated, and a list of sites is appended.

DER WIENERWALD. *Eine Landeskundliche Darstellung. Forschungen zur Landeskunde von Niederösterreich Band 1/2.*

By Anton Schachinger. Ferdinand Berger, Horn. 9½ x 6¾; viii + 510 + 18 plates; 1934 (paper).

Beginning with the geological structure of the Wienerwald, its topography, climate, fauna and flora (all of which are covered in the first 82 pages), the author proceeds with the history of the populations inhabiting it. He traces the vicissitudes of the people and their culture from prehistoric times through the Roman period and the various Magyar and Turkish invasions, to the present. Information concerning religious history, plans of towns, constructions of roads, industries, etc. are given. It is a detailed, scholarly, well-documented work. It is illustrated with photographs and several maps, and has an index of place names.

HUMAN STERILIZATION TO-DAY. *A Survey of the Present Position.*

By Cora B. S. Hodson. Watts and Co., London. 1 shilling (cloth); 7d. (paper). 7¼ x 4⅞; vii + 56; 1934.

An ardent but on the whole sane plea for permissive sterilization. The first chapter consists of a good explanation, for the lay reader to whom the book is addressed, of eugenic sterilization. The author has visited many places where eugenic sterilization is being done and reports some of these in considerable detail. Throughout the book no inkling is given that the determination of the hereditary aspect of any defect may not be easy and clear cut.

THE LUMMI INDIANS OF NORTHWEST WASHINGTON.

By Bernhard J. Stern. Columbia University Press, New York. $2.00. 10 x 6½; 125 + 6 plates; 1934.

The Lummi Indians are now settled on a reservation near the Canadian border in northwestern Washington. Because of the tribe's geographic isolation the Lummi culture has remained quite intact and the present studies are based on ethnological material collected in 1928–29. The book is divided into three parts: Part 1, dealing with the cycle of life and describing important stages in the development and relationships of the individual, relative to his fellows; Part 2, entitled "Tribal Culture" describing many of the customs and activities of the Lummi society, and Part 3, depicting the legends and lore of these people. This is an interesting and valuable contribution to American Indian ethnology.

RACIAL CONTACTS AND SOCIAL RESEARCH. *Papers Presented at the Twenty-eighth Annual Meeting of the American Sociological Society, Held at Philadelphia, Pennsylvania, December 27–30, 1933. Volume XXVIII, The American Sociological Society.*

The American Sociological Society. The University of Chicago Press, Chicago. $1.50. 9⅜ x 6⅝; viii + 129; 1934 (paper).

A group of some 68 papers on various sociological problems by American sociologists presented at the twenty-eighth annual meeting of the American Sociological Society. Reports are made from sections of: Human Ecology, Social Psychology, Social Institutions, Rural Sociology, Teaching of Sociology, The Community, Sociology of Religion, Social Work, Social Statistics, Educational Sociology, The Family, and Sociology and Psychiatry.

THE RACIAL MYTH.

By Paul Radin. Whittlesey House, McGraw-Hill Book Co., New York. $1.50. $7\frac{3}{8}$ x 5; ix + 141; 1934.

In this book Professor Radin of the Department of Anthropology of the University of California ridicules the idea that the development of civilization is bound up with any one race. Neanderthal man, who first invented stone implements, was probably not an ancestor of any of our present races. The inventors of pottery were members of the white race; the Egyptians, a mixed white race, invented glass and the Chinese invented porcelain. And so it goes. The development of civilization is an inextricably interwoven record of the achievements of many races.

THE JEW IN SCIENCE.

By Louis Gershenfeld. The Jewish Publication Society of America, Philadelphia. $2.75. $8\frac{1}{2}$ x $5\frac{3}{8}$; vii + 224; 1934.

About half of this book is devoted to short biographical lists of Jewish scientists of modern times in the various scientific fields. The rest of the space is concerned with the relation of Jewish people to national development up to and through the Renaissance. The author hopes to change distorted views about the Jew in science and to encourage a desire among Jews to learn something of their brethren in the scientific field. The book has therefore at times a slightly propagandist tone that is somewhat irritating.

THE LIFE OF SIR ROBERT JONES.

By Frederick Watson. William Wood & Co., Baltimore. $3.75. $8\frac{3}{4}$ x $5\frac{3}{4}$; 327 + 10 plates; 1934.

A charming man Sir Robert must have been, but hard to keep up with. The amount of work this famous orthopedic surgeon managed to accomplish was almost superhuman. His associates and colleagues must have been exceptional to make such feats possible although little is said of that. The early chapters showing the influence of his father and uncle on the young man are particularly entertaining.

A VOYAGE ON THE SEALER EMELINE AND THE JOURNAL. *From Washington Fosdick's Manuscript Preserved in the Museum of the Old Dartmouth Historical Society at New Bedford. Zoologica, Vol. 9, No. 14.*

Edited by Arthur C. Watson. New York Zoological Society, New York. 85 cents net. $9\frac{1}{2}$ x $6\frac{3}{4}$; 75; 1931 (paper).

Interesting alike to the biologist and the student of Americana. To the former because of the information on the numbers and habits of seals in the 1840's; to the latter because of the side-lights it gives us in these effete times on what men could do. The cold, wetness, and general hard work involved in procuring seal oil is almost unbelievable.

THE YOUTH OF OLD AGE.

By Johnson Brigham. Marshall Jones Co., Boston. $2.50. 8 x $5\frac{3}{8}$; xvi + 209; 1934.

The author of this anthology that isn't an anthology was born in 1846 and he feels strongly that old age need not be the bleak and distasteful thing most people believe inevitable. To bolster up his own courage, perhaps, he has here gathered together all sorts of quotations dealing with the delights and benefits of advancing years. There is as much of Brigham's comment about the authors quoted as there is actual quotation.

A BIBLIOGRAPHY OF GILBERT WHITE. *The Naturalist and Antiquarian of Selborne. With a Biography and a descriptive Account of the Village of Selborne.*

By Edward A. Martin. Halton and Company, London. 10s. 6d. $8\frac{1}{2}$ x $5\frac{3}{8}$; viii+ 195; 1934.

In this enlarged and revised edition the bibliography is brought up to date and two pen and ink sketches of White, found in his copy of Pope's *Iliad*, are reproduced.

QUARTERLY BULLETIN OF THE HEALTH ORGANISATION, *League of Nations, Vol. 3, Nos. 1 and 2.*

World Peace Foundation, 40 Mt. Vernon St., Boston; League of Nations, Geneva. 65 cents each (subscription $2.50 per year) (U. S. A.); 2 shillings each (10 shillings per year) (Geneva). 9½ x 6¼; No. 1, 155; No. 2, 168 + 13 plates; 1934 (paper).

ZOÖLOGY

THE WOOD-FEEDING ROACH CRYPTOCERCUS, *Its Protozoa, and the Symbiosis between Protozoa and Roach. Memoirs of the American Academy of Arts and Sciences, Vol. 17, No. 2.*

By L. R. Cleveland, In collaboration with S. R. Hall, Elizabeth P. Sanders, and Jane Collier. George Banta Publishing Co., Menasha, Wisconsin. $6.50. 11¾ x 9¾; x + 160 + 60 plates; 1934.

For approximately the last decade Cleveland has been describing the symbiotic relationships between cellulose-feeding termites and their cellulose-digesting intestinal flagellates. In the present monograph he extends his researches by studying the same problem for the wood-feeding roach *Cryptocercus punctilatus* Scudder. The latter organism is a happy choice due to its phylogenetic affinities with the termites and to technical advantages, such as relatively large size, ease in laboratory breeding, etc. The following topics are dealt with in detail: first, the structure of the alimentary canal of the roach; second, a taxonomic and morphologic discussion of the intestinal flagellates of *Cryptocercus* including many interesting observations upon protozoan mitosis, and third, a consideration of the symbiosis between roach and protozoa. Under the last division Cleveland describes the techniques used in defaunating and reinfecting the roaches with their protozoa; the production and function of the protozoan-elaborated enzyme, cellulase, which digests cellulose into dextrose, and the way in which the dextrose is finally absorbed by the roach.

The problem is studied from the natural history as well as the experimental side, which is a virtue. In discussing the experimental material one feels that more explicit statements as to number of cases and statistical significance of the results would be advantageous. On the whole, however, a large and important problem has been approached with interesting results presented and with new problems suggested.

THE FUR SEAL OF THE CALIFORNIA ISLANDS *With New Descriptive and Historical Matter. Zoologica, Vol. 9, No. 12.*

By Charles H. Townsend. New York Zoological Society, New York. 60 cents net. 9½ x 6¾; 17; 1931 (paper).

THE FUR SEAL OF THE GALAPAGOS ISLANDS. *Zoologica, Vol. 18, No. 2.*

By Charles H. Townsend. New York Zoological Society, New York. 60 cents. (postage extra 5 cents). 10⅝ x 7; 14; 1934 (paper).

These two papers treat two southern fur seals which are now practically extinct. The first gives descriptive and historical matter concerning *Arctocephalus townsendi.* They inhabited the islands off the coast of Southern California and in the 1800's had a great commercial importance. However, little is known about them, and when the author was sent to Guadalupe Island in 1892 to identify the species he found but seven, although between 1876 and 1892 not less than 5,575 were reported taken from this and the San Benita Islands.

The *Arctocephalus galapagoensis* is the subject of the second paper. The text is brief and is based on several seals captured in 1932 and '33 and presented to the Zoological Garden at San Diego, California. These are the only specimens taken since 1906 when a single one was procured. The primary object of the paper was the publication of eleven photographs taken in San Diego, in order to show naturalists what this seal actually looked like.

REPTILES AND AMPHIBIANS. *Their Habits and Adaptations. Revised Edition.*

By Thomas Barbour. Illustrated in part by George Nelson. Houghton Mifflin Co., Boston. $4.00. 9 x 5⅝; xx + 129 + 27 plates; 1934.

Regarding the first edition of this book we remarked (Volume 3, page 139) that it "is an example of the highest type of popular natural history writing" and there is no need to modify that opinion now. It is a splendidly arranged introduction to the principal characteristics of living reptiles and amphibians and to the variety of modifications of structure and behavior to be found in this group of animals and it is unusually well illustrated. It ought to accomplish its avowed purpose of turning the attention of naturalists to an interesting group of animals for which information on life histories is incomplete. There is an index and an annotated bibliography in which the merits and demerits of individual books, papers, and authors are mentioned with more than usual candor.

ANIMALIUM CAVERNARUM CATALOGUS. *Pars I.*

By Benno Wolf. W. Junk, Berlin. 18 marks. 10 x 7½; xxiii + 112; 1934 (paper).

This catalogue of cavern fauna of the world will be issued in several numbers, each to be divided into three parts as follows: I. Bibliography; II. Catalogue of caves, large enough for man to enter, listed by continents and countries, with mention of the fauna found in each; III. Catalogue of fauna, taxonomically classified, with the caverns in which each is found given. The first number includes authors from A to Ch, caves in Belgium, Bulgaria, and Germany, and the phyla, Protozoa, Porifera, Coelenterata, Vermes, and Arthropoda. It is a very thorough and systematic piece of work.

THE COLLARED LIZARD: *A Laboratory Guide. By D. Dwight Davis. The Macmillan Company, New York.* 90 cents. 7⅜ x 4⅞; viii + 57; 1934.

A laboratory manual dealing with the comparative morphology of the collared lizard, *Crotaphytus collaris*, of the southwestern United States. About this form the author says;

> I believe that the choice of the collared lizard as a representative of the class Reptilia is a happy one. Certainly the fundamental characters of the group are less masked by confusing specializations in the lizards than in any other of the common reptilian groups. This abundant terrestrial iguanid probably conforms as nearly to the ideal lacertilian type as any available form. Moreover, in size it is eminently suited to class dissection.

TROPICAL FISH & THEIR CARE.

By Norbert Lederer. Alfred A. Knopf, New York. $2.50. 7½ x 5; xxi + 229; 1934.

Here is a book destined for piscatorial popularity; a concise and organized treatment of tropical fish and their problems. The book is planned for both immature and mature aquarists and deals with such problems as feeding, breeding, and tank equipment as well as presenting a discussion of the many kinds of tropical fish suitable for aquarium use. The reviewer will be pardoned if, in his ignorance, he fails to see how some of the therapeutic measures advocated for fish diseases can be successful.

GENERAL ZOOLOGY.

By Frederick H. Krecker. Henry Holt and Co., New York. $3.50. 8⅜ x 5½; xi + 634; 1934.

Another text-book of zoölogy for first-year college students. There are four divisions to the subject matter; first, 'A typical animal'; second, 'A review of the animal kingdom'; third, 'Animals and their environment,' and, fourth, 'The origin of animals.' The volume is well illustrated. The chief merit of the book lies in its simplicity of statement and organization. As the author hopes, it probably will be useful in general zoology courses where the majority of the students merely wish biological orientation and are not interested in specialization.

LES INVERTÉBRÉS (*Cœlentérés et Vers*). *Actualités Scientifiques et Industrielles 133. Leçons de Zoologie et Biologie Générale, III.*

By Georges Bohn. Hermann et Cie, Paris. 15 francs. 10 x 6½; 102; 1934 (paper).

A text-book type of discussion of the coelenterates, sponges, annelids, platyhelminthes, nematodes, and aberrant worms. The reproductive and life-cycle aspects are stressed. The book is illustrated but not profusely so. The reviewer was not greatly impressed by this book. Much seems to have been lost by separating a few invertebrate phyla from their many relatives and reporting on them in so little detail. The volume can not be considered a reference work, and, due to the separation of the phyla, loses much of its value as a general zoological text.

GROWTH AND AGE IN THE GIANT TORTOISE OF THE GALAPAGOS. *Zoologica, Vol. 9, No. 13.*

By Charles H. Townsend. New York Zoological Society, New York. 35 cents net. 9½ x 6¾; 16; 1931 (paper).

The principal conclusion is that:

> The common supposition that large Galapagos tortoises must be of great age is unwarranted. Under natural conditions and especially under *favorable* climatic conditions in captivity, they reach a large size in a few years, when the rate of growth becomes slow. There are records of both Galapagos and Aldabra giant tortoises that lived under observation in tropical climates more than 150 years, when their lives ended upon removal to cold climates. The real length of life is unknown. Certain museum specimens known to have exceeded 500 pounds at death, were doubtless very old.

THE MOOSE OF ISLE ROYALE. *University of Michigan, Museum of Zoology,, Miscellaneous Publications No. 25.*

By Adolph Murie. University of Michigan Press, Ann Arbor. 10 x 6¾; 44 + 6 plates; 1934 (paper).

Although the author gives a good description of the moose and their behavior, as observed by himself, particular emphasis is placed on their feeding habits. They are so numerous on Isle Royale in Lake Superior that overbrowsing is general. In order to preserve the landscape the author recommends drastic reduction of the moose population on the island and offers several suggestions for reducing the number. The pamphlet contains several photographs of the animals and their ravages on the vegetation.

THE WEASELS OF NEW YORK. *Their Natural History and Economic Status.*

By W. J. Hamilton, Jr. The University Press, Notre Dame, Ind. 9 x 6; 86; 1933 (paper).

This pamphlet, a reprint of a paper published in the *American Midland Naturalist* (Vol. 14, 1933) deals with two weasels found in New York State: *Mustela noveboracensis*, commonly known as the New York weasel, and *Mustela cicognanii*, or Bonaparte. Besides a description of these species and their life history, there is a short section on the value of the weasel as a fur product, and as a rat and mouse predator, one on its care in captivity for study purposes, a bibliography and several illustrations.

ODDLY ENOUGH. "*From Animal Land to Furtown.*"

By Arthur Samet. "Oddly Enough," 106 West 30th St., New York. $2.00. 9¼ x 6¼; 200; 1934.

The author admits in the foreword that "this work is a curious study in furs," and that is, if anything, an understatement. The book is a jumble of elementary zoological facts, odd child-like pen and ink drawings, fairy tale references, and etymology written by a fur dealer. One feels the author is only on firm ground when he is discussing the classification of furs from the dealer's standpoint. Otherwise the book is of little merit.

GROWTH OF DIAMOND-BACK TERRAPINS: *Size Attained, Sex Ratio and Longevity. Zoologica, Vol. 9, No. 15.*

By Samuel F. Hildebrand. New York Zoological Society, New York. 20 cents net. 9½ x 6¾; 13; 1932 (paper).

The size attained, sex ratio and longevity of the diamond backed terrapin is discussed briefly. In nature, this form frequently reaches a length as great as seven inches for the females. No precise data are available as to the length of life although the author, "regards the estimate of the highest age of forty years . . . . as much too low."

THE NATURALIST ON THE PROWL.

By Frances Pitt. The Macmillan Co., New York. $2.00. 7½ x 5⅛; x + 137 + 33 plates; 1934.

Miss Pitt, an enthusiastic nature lover, gives much practical advice on the necessary equipment for studying wild life and on methods of observation. She also includes many of her own experiences with birds and beasts in her field work in the British Isles. The volume is well illustrated with the author's excellent photographs, contains a list of species mentioned (21 mammals, 73 birds, 2 insects) with scientific names and an index.

DIGITAL EPIPHYSES AND CARPAL BONES IN THE GROWING INFANT FEMALE GORILLA WITH SITTING HEIGHT, WEIGHT AND ESTIMATED AGE. *Zoologica, Vol. 11, No. 5.*

By Charles V. Noback. New York Zoological Society, New York. 90 cents net. 9½ x 6¾; 35; 1930 (paper).

The most prominent feature of this little pamphlet is the X-ray record of the growth changes in the bones of the hand of the gorilla. Certain other data on growth of the animals are also given. The work is based on five animals, one of which was living and was observed over two years time.

THE LITTORAL CRUSTACEAN FAUNA OF THE GALAPAGOS ISLANDS. *Part II. Anomura. Zoologica, Vol. 14, No. 1.*

By Lee Boone. New York Zoological Society, New York. 60 cents + postage. 9½ x 6¾; 62; 1932 (paper).

The author presents a description and illustration of every species of anomuran crustaceans known from the littoral zone of the Galapagos Islands, including the larval forms of three species of Porcellanids which are the first American anomuran *Magalops* to be described.

TRAITÉ DE ZOOLOGIE. *Index Alphabétiques de l'Ouvrage Complet (10 Fascicules).*

By Edmond and Rémy Perrier. Masson et Cie, Paris. 40 francs. 10 x 6½; 163; 1933 (paper).

This index will be welcomed by those who already own the previous ten fascicules of this excellent reference series, several numbers of which have been noticed at various times in these columns. Two indices are contained in this number—one of technical terms and one of names of species and groups.

NOTES ON THE GILL-FINNED GOBY. *Bathygobius soporator (Cuvier and Valenciennes).*

By William Beebe. New York Zoological Society, New York. 40 cents net. 9½ x 6¾; 12; 1931 (paper).

The author sums up in his usual interesting manner, his observations on the goby, *Bathygobius soporator*. The pamphlet is illustrated by drawings, and a colored plate showing the color phases of this fish.

TROPICAL FISH.

By Lucile Q. Mann. Leisure League of America, 30 Rockefeller Plaza, New York. 25 cents. 8 x 5½; 99; 1934 (paper).

A real bargain, this. As much for twenty-five cents as could be found in a long day. This is really an excellent little treatise containing just the things an amateur wants to know about parlor fish and written in an extremely interesting and pleasing way.

CAVE LIFE OF KENTUCKY. *Mainly in the Mammoth Cave Region.*

By Vernon Bailey, with chapters on The Birds, by Florence M. Bailey, and on The Invertebrates, by Leonard Giovannoli. The University Press, Notre Dame, Ind. $1.25. 9 x 6; 256; 1933.

An account of the life habits, appearance, numbers and frequency of occurrence, and a classification of the different species of mammals, birds, reptiles and amphibians found in the caves, with special reference to Mammoth Cave, Kentucky.

THE MAMMALS OF SOUTHERN NEVADA. *Transactions of the San Diego Society of Natural History, Vol. 7, No. 36.*

By William H. Burt. Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 53; 1934 (paper).

After a brief account of the physiography, floral and faunal relations in southern Nevada, the author presents a list of mammalian species, with descriptions, found in this region.

THE AMPHIBIANS OF KANSAS. *The American Midland Naturalist, Vol. 15, No. 4.*

By Hobart M. Smith. University of Notre Dame, Notre Dame, Ind. 35 cents. 9 x 6; 152; 1934 (paper).

A taxonomic discussion of the species of amphibians inhabiting the central plains region. Special consideration is given those found in Kansas.

NOTES ON SOME TYPES OF NORTH AMERICAN BIRDS. *Transactions of the San Diego Society of Natural History, Vol. 7, No. 30.*

By A. J. van Rossem. Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 15; 1934 (paper).

WEST AMERICAN SPECIES OF THE GENUS LIOTIA. *Transactions of the San Diego Society of Natural History, Vol. 7, No. 37.*

By A. M. Strong. Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 23; 1934 (paper).

A REVIEW OF THE RACES OF GEOCOCCYX VELOX. *Transactions of the San Diego Society of Natural History, Vol. 7, No. 39.*

By Robert T. Moore. Society of Natural History, San Diego, Calif. 10⅛ x 6⅞; 15; 1934 (paper).

THE PRIMITIVE PERSISTS IN BIRD LIFE OF YELLOWSTONE PARK, *By George M. Wright.* A WILDERNESS-USE TECHNIQUE, *By Ben H. Thompson. The Condor, Vol. 36, pp. 145–157.*

Wild Life Division, National Park Service, Berkeley, Calif. 10½ x 7¼; 12; 1934.

BOTANY

THE LIFE FORMS OF PLANTS AND STATISTICAL PLANT GEOGRAPHY. *Being the Collected Papers of C. Raunkiaer.*

Oxford University Press, New York. $14.00. 9¾ x 6¼; xvi + 632 + 35 plates; 1934.

A valuable service has been rendered to ecologists by collecting Professor Raunkiaer's papers from the somewhat inaccessible journals in which they were published and in translating them from Danish into English, for his principles of classification of the life forms of plants will certainly be widely applied as they become better known. Raunkiaer's best-known scheme for statistical analysis of plant communities is to divide vascular plants into categories according to the amount and kind of protection afforded to the buds and shoot-apices. In his earlier work he recognizes ten categories, later only five: Phanerophytes, plants whose buds survive the unfavorable season freely exposed to the weather; Chamaephytes, whose buds are carried close to the ground; Hemicryptophytes, whose buds are situated in the soil surface; Cryptophytes, whose buds are buried in the soil; and Therophytes, which survive the unfavorable season as seeds. This forms a graded series "of which each successive member is on the whole better adapted to survive unfavorable seasons." He obtains a biological spectrum of the flora of a region by calculating the percentages of the flora that fall into the several classes, and this gives him a simple means of comparing one region with another, especially after he determined the distribution of forms in a random sample of 1000 species taken from the *Index Kewensis*.

Raunkiaer analyzed the floras of a large number of regions in this way and made valuable contributions to plant geography. All of his ecological work had a statistical basis and he developed many new procedures for obtaining numerical charac-

terizations of plant communities that deserve attention. The translation has been smoothly done, there are bibliographies, and there is a good index.

THE FAMILIES OF FLOWERING PLANTS. II. MONOCOTYLEDONS. *Arranged According to a New System Based on Their Probable Phylogeny.*

By J. Hutchinson. Macmillan and Co., London and New York. $6.00. $8\frac{5}{8}$ x $5\frac{5}{8}$; xiii + 243; 1934.

This book is intended

> to provide the student with descriptions of the families of Monocotyledons arranged in as logical a sequence as may be possible according to their probable phylogeny, starting with the most primitive and ending with the most advanced types. Some alterations in the status of a few of the families are proposed here for the first time, especially that of the *Amaryllidaceae* and of the *Liliaceae*.

The author proposes a system of classification which differs from the Engler and Prantl and other systems in more respects than we have space to mention and argues very persuasively for his point of view. The Monocots, which are considered to be monophyletic in origin and probably derived from the Ranales, are divided into three major groups on the basis of calyx and corolla characteristics: the Calyciferae have the Butomales and Alismatales as the most primitive members and the Bromeliales and Zingiberales as the most advanced; the Corolliferae begin with the Liliales and their allies and end in the Orchidales; and the Glumiflorae include the Juncales, Cyperales, and Graminales. The Liliales, in particular, have been thoroughly rearranged. This volume is constructed on the same principles as the first volume dealing with Dicots previously reviewed (Volume 1, p. 455) and, similarly, has natural and artificial keys to families, numerous illustrations of plants of phylogenetic importance, maps, and an index to families and genera. In this volume, in addition, there are keys to the genera of all families except the Gramineae and Orchidaceae, which add greatly to its usefulness. It is in every way an important book.

THE GRAMINEAE: *A Study of Cereal, Bamboo, and Grass.*

By Agnes Arber. Macmillan Co., New York. $8.50. $9\frac{1}{4}$ x $6\frac{1}{4}$; xvii + 480; 1934.

This comparative morphological study of the Gramineae is written by one of the foremost authorities in the field, and represents the results of careful examination, organ by organ, and tissue by tissue, of representative members of the order at every stage in their life history from seedling to flower, with the object of finding what peculiarities of structure and what modifications of function characterize the group as a whole. It is written in the style of Mrs. Arber's earlier monographs on the monocotyledons and the water plants and is as abundantly illustrated. Part of the material has been published in the *Annals of Botany*. This only half-way describes the book, however. One of the most significant things about the order is that man has depended on cereals, bamboo, and grass for food and shelter for himself and his domestic animals for as long a period as anything is known about human activities, and Mrs. Arber has set down the things about the relation of the grasses to man that, as she says, happened to interest her. This is a quaint form of understatement. Actually, she has drawn extensively from a wide variety of sources; the records of antiquity, herbals, traveler's accounts (particularly for information about bamboo), agronomy, and a number of other branches of science, and the result has been to make it a book of unusual interest and one that every biological library ought to have. There is an index and a bibliography that are models of completeness.

THE THEORY AND PRACTICE OF SILVICULTURE.

By Frederick S. Baker. McGraw-Hill Book Co., New York. $5.00. 9 x $5\frac{3}{4}$; xiv + 502; 1934.

A textbook of forestry has to take account of the fact that forestry is as much a branch of economics as a field of applied biology and that in addition to this limitation, which all branches of applied science share, it calls for expert long-range fore-

casting of the results of a treatment that will be ended 50 or 100 years later. This book seems to be admirably well adapted to the nature of the subject and to be pedagogically sound. The plan is to survey the basic fields of knowledge upon which foresters may draw, including plant physiology and forest ecology, to indicate what practices are desirable from a theoretical standpoint and which are economically feasible, and to discuss silvicultural practices in the different forest regions of the United States. There is an extensive bibliography and an excellent index.

IDENTIFICATION OF THE COMMERCIAL TIMBERS OF THE UNITED STATES.

By H. P. Brown and A. J. Panshin. McGraw-Hill Book Co., New York. $3.00. 9 x 5¾; xxvi + 223; 1934.

This book, the first of a new series of forestry textbooks, has two analytical keys for the identification of wood, one based on characters seen with the naked eye or with the aid of a hand lens, and the other based on anatomical characters visible in prepared sections under a compound microscope. Each key is illustrated by a set of excellent photomicrographs, about 270 in all, of transverse and tangential sections taken at magnifications of 5x or of 75x. One section is devoted to descriptions of the visible characters and anatomical structure of the woods of 90 species. In an introductory chapter there is a brief introduction to wood anatomy intended for people without previous botanical training, and the book closes with a glossary and a good index.

DIE TYPENLEHRE IN DER MIKROBIOLOGIE. *Ihre Grundlagen und ihre Bedeutung für die Epidemiologie, Klinik und Therapie.*

By Max Gundel. Gustav Fischer, Jena. 8 marks (paper); 9 marks (cloth). 9⅛ x 6⅜; viii + 192; 1934.

This book was written with a two-fold purpose, to indicate to the clinician the current status of knowledge of the groups of bacteria of presumably sub-specific rank which have such different degrees of pathogenicity as to merit special consideration, and, for the benefit of bacteriologists and immunologists, to summarize the work that has been done on the discrimination of bacterial races and types by cultural and biochemical methods. Only bacteria pathogenic to man are discussed and the list includes most of the major groups of pathogens. There is an author index and a bibliography of nearly 350 titles.

DIAMETRAL CHANGES IN TREE TRUNKS. *Carnegie Institution of Washington Publication No. 450.*

By Ferdinand W. Haasis. Carnegie Institution of Washington, D.C. $1.50 (paper); $2.00 (cloth). 10 x 6⅞; 103; 1934.

On dry days the shrinkage in diameter of the trunk of North American forest trees may amount to 1/500 or even 1/100 of the diameter of the tree; when an adequate water supply is again available swelling takes place quickly. Besides dry weather several other factors can cause shrinkage, among them the development of new foliage and wounding. Haasis has classified the dendrographic records obtained at the Desert and Coastal Laboratories of the Carnegie Institution, where most of this kind of work has been done, and has summarized the results of other workers. His book is too over-burdened with details to make for easy reading, but it is a good summary of the present status of the subject, and there is an extensive bibliography.

FIELD STUDIES IN ECOLOGY.

By R. Bracher. J. W. Arrowsmith, London. 2s. 6d. 7⅛ x 4¾; 100; 1934.

This little book is intended to lighten the task of college teachers organizing a course in ecology and it corresponds, roughly, to the laboratory manuals in use in other biological sciences. The principal plant communities of the British Isles are described briefly and there are short lists of the principal species to be found in each. The field methods a beginning class in

ecology can carry out are described in some detail and are illustrated by maps and diagrams. Although this was not written for our flora it ought to be a very useful book for American ecology teachers. There is a good index.

TREES OF THE SOUTHEASTERN STATES. *Including Virginia, North Carolina, South Carolina, Georgia and northern Florida.*

By William C. Coker and Henry R. Totten. University of North Carolina Press, Chapel Hill. $2.00. $7\frac{3}{4}$ x $4\frac{7}{8}$; vi + 399 + 3 plates; 1934.

An extremely useful work for all those, whether layman or student, who are interested in the native forests, naturalized trees and large shrubs of our southeastern states. The descriptions are in simple terms; the keys will not be difficult for the inexperienced to understand; typical leaves, flowers and fruits are illustrated of nearly all the species described; and, in many cases suggestions are made as to the desirability of the trees for use in ornamental planting. A bibliography, a glossary and an index are included in the volume.

THE PLANKTON ALGAE OF THE WEST END OF LAKE ERIE.

By Lewis H. Tiffany. Ohio State University Press, Columbus. $9\frac{3}{4}$ x $6\frac{3}{4}$; 112; 1934 (paper).

This is a list, with descriptions, of the plankton algae found along the western shore of Lake Erie and in bodies of water on numerous islands in the west end of the lake. It includes some species not previously described elsewhere. A bibliography, an index and 15 plates picturing 364 varieties add to the usefulness of this contribution.

COMMENTATIONES FORESTALES 6. *Die Technischen Eigenschaften der Birke Lettlands.*

By Rob. Liepiņš. Society of Forestry in Suomi, Helsingfors, Finland. $9\frac{3}{4}$ x $6\frac{1}{4}$; 15; (1933).

ACTA FORESTALIA FENNICA 40. *Suomen Metsätieteellisen Seuran 25-Vuotis-Juhlajulkaisu (Special Issue on the Occasion of the 25 Years' Jubilee of the Society of Forestry in Suomi).*

Society of Forestry in Suomi, Helsingfors, Finland. $9\frac{1}{2}$ x $6\frac{3}{8}$; x + 901; 1934 (paper).

MORPHOLOGY

THE AUTONOMIC NERVOUS SYSTEM. *Second Edition, Enlarged and Thoroughly Revised.*

By Albert Kuntz. Lea and Febiger, Philadelphia. $7.50. $9\frac{1}{4}$ x $5\frac{5}{8}$; 697; 1934.

There is little to add to our notice of the first edition (Vol. 5, p. 251) except that the subject matter has been brought up-to-date. The chapters have the same titles but considerable internal change is evident.

"The new findings bearing on certain phases of the functional activity of the autonomic system have called for a critical reëxamination of many generally accepted concepts which, in some instances, has resulted in a changed point of view, and, we trust, a better understanding. In the preparation of the second edition, the text has been revised in the light of the more recent studies and an attempt has been made as far as possible, to incorporate all the more important findings, without materially increasing the size of the volume."

DEVELOPMENTAL ANATOMY. *A Text-book and Laboratory Manual of Embryology.*

By L. B. Arey. W. B. Saunders Co., Philadelphia. $6.50. $9\frac{3}{4}$ x $6\frac{3}{8}$; ix + 593; 1934.

This standard American textbook for students of human embryology has been revised, in its third edition, by rewriting much of the text matter, adding 181 new illustrations, and bringing the discussions into line with latest findings. The book is so well known to anatomists, zoölogists and medical students that further discourse here would seem superfluous.

A TEXTBOOK OF HISTOLOGY. *Second Edition, Completely Revised.*

By Alexander A. Maximow and William Bloom. W. B. Saunders Co., Philadelphia. $7.00 net. $9\frac{3}{4}$ x $6\frac{1}{4}$; xiv + 662; 1934.

The first edition of this text was noticed

in these columns (Vol. 6, p. 242). The book has now been recast by the original editor and made smaller and more useable for beginning students of medicine. The section on the nervous tissue was again written by Prof. C. J. Herrick. The book is to be recommended.

PHYSIOLOGY AND PATHOLOGY

PAPERS OF CHARLES V. CHAPIN, M.D. *A Review of Public Health Realities. Selected by Frederic P. Gorham. Edited by Clarence L. Scamman. The Commonwealth Fund, New York.* $1.50. 8¾ x 5⅛; xxiv + 244; 1934.

In this book sixteen of Dr. Chapin's most important papers in the field of public health are reprinted. The first six papers, under the heading of public health administration, relate "to the dangers of indiscriminate and hasty publication, to the wise expenditure of public funds, and to the assimilation and use of new scientific knowledge and technique." A second group of five papers, on the control of communicable disease, are representative of scientifically sound and thoroughly practical views on the importance of aseptic nursing, hospital isolation, the identification of carriers, the reporting and recording of cases, the importance of personal cleanliness which are today the essence of protection against communicable disease. The last group of five papers, under the title epidemiology and vital statistics, are typical of Dr. Chapin's contributions in the field of quantitative methodology. In addition to the reprints, the volume contains a well written foreword which may be expected to stimulate in the most casual reader an interest in public health work, a short biographical sketch, and a complete bibliography of the books and articles (133 references) by Dr. Chapin. High commendation should be extended to the persons responsible for the republication of these scattered and not easily available papers. The book profitably can be read by every person truly interested in public health work. It is a particularly appropriate title to be included in the collateral reading list of medical students today.

CELLULAR RESPIRATION. *By Norman U. Meldrum. Methuen and Co., London.* 3s. 6d. net. 6¼ x 4¼; xi + 116; 1934.

A young investigator at Cambridge University, who did not live to see the publication of his book, has written an extraordinarily clear, brief exposition of the present status of our knowledge of intracellular oxidations and reductions that ought to be of uncommon usefulness to any student of the subject. His temper is critical, but it is not the sort of criticism that leads to the impression that the research in question would have been better done if the author had done it; it is rather the careful sorting out of certain relevant facts from a highly specialized field of research to form a plausible physiological system. It is written for graduate students in physiology. It is provided with a better glossary than could have been expected, a good index, and with short bibliographies at the end of each chapter.

LA CELLULE GERMINALE DANS LE DYNAMISME DE L'ONTOGENÈSE. *Actualités Scientifiques et Industrielles 119. Exposés de Biologie, La Cellule Germinale dans l'Ontogenèse et l'Évolution, I.*

By Vera Dantchakoff. Hermann et Cie, Paris. 18 francs. 10 x 6½; 87; 1934 (paper).

A series of well conceived experiments regarding the development of germ cells and its relation to that of the gonads are here reported. The author has proceeded to a localized destruction of embryonic tissue (of bird embryos mostly) and of the germ cells by x-rays. As a consequence she observed that in the absence of germ cells the gonads are not formed nor the metanephros differentiated. The primordial germ cells, she concludes, are an important factor in morphogenesis of the developing organs. There is an excellent critical review of the literature and the author has succeeded in presenting her

results as a logical sequence of the work of others.

PARASITISM AND DISEASE.

By Theobald Smith. Princeton University Press, Princeton, N. J. $2.00. 8½ x 5½; xiii + 196; 1934.

The relationship between disease and parasitism in its broadest aspects, incorporating the author's unpublished Lowell lectures for 1909 and Herter lectures for 1916, reach final publication in these, the Vanuxem lectures. Bringing to bear upon the problem a wealth of research experience and an intimate personal acquaintance with modern developments Dr. Smith (whose lamented death is an irreplaceable loss to American science) here puts together, as a unified whole, all that is known of the struggle of man and the higher animals against infectious and invasive diseases.

ESSAI DE CLASSIFICATION DES SUBSTANCES SYMPATHICOMIMÉTIQUES. *Actualités Scientifiques et Industrielles, 135. Exposés de Physiologie, III.*

By Z. M. Bacq. Hermann et Cie, Paris. 8 francs. 10 x 6½; 24; 1934 (paper).

The author classifies what he calls sympathomimetic substances into perfect and imperfect. His criterion for differentiation is that the former through their intimate physico-chemical and physiologic properties simulate perfectly the functions of the sympathetic system while the latter instead only partially simulate them and then only through physico-chemical excitations of the post-ganglionic fibres. In the first group he places adrenaline and sympathin, in the second, ephedrin, tyramine, and amylamine.

ASSOCIATIONS FONCTIONNELLES *et Milieu Intérieur. Actualités Scientifiques et Industrielles, 155. Leçons de Zoologie et Biologie Générale, V.*

By Georges Bohn. Hermann et Cie, Paris. 15 francs. 10 x 6½; 89; 1934 (paper).

In this volume of his *Leçons* the eminent author presents an outline of the present knowledge regarding polarity, regeneration and tropisms; development of the bony skeleton; properties and composition of the blood and hormones; development of the central nervous system, muscular contraction; the functions of the urogenital system. Well written, with emphasis only on what has definitely been proven, this book should be useful to students of biology.

HYGIENE FOR FRESHMEN.

By Alfred Worcester. Charles C Thomas, Springfield. $1.50. 8¾ x 5¾; vii + 151; 1934.

This book gives the substance of a half-year weekly lecture course in Hygiene given to Harvard freshmen. Nine lectures are devoted to very elementary considerations of general biology and human physiology, three deal with mental hygiene, disease prevention and immunity. Questions at the end of each chapter indicate what the author hopes the student will remember. There is a two page glossary and an index.

LA CELLULE VIVANTE. *Physiologie et Pathologie Cellulaires.*

By E. M. Poletti. Translated by Gaullieur l'Hardy. Gaston Doin et Cie, Paris. 25 francs. 9½ x 6¼; ii + 133; 1934 (paper).

A very interesting presentation of facts and theories regarding cellular physiology and pathology. The author manifests uncommon erudition and his exposition is succinct and justly critical. The lack of a bibliography is to be deplored.

THE LANGHAN'S CELLULE ABERRATED IS THE SPECIFIC CELLULE OF CANCER. *The Matrix Embryonic Cellule of the Primal Syncytium, the Langhan's Cellule; Its Great Importance Throughout Life; Especially in the Early Days of Ovum Life. The Cohenheim Theory. The Cellulettes. Syncytioma. The Pre-Cancerous Carcinoids. Teratomata. An*

Illustrated Review of Some Primal Embryology, 2–8th Week, Including the Normal and Abnormal Cancer Cellule.

By Frank A. Stahl. Frank A. Stahl, Hamilton Club, Chicago. Free. 9¼ x 6; 154; 1934 (paper).

BIOCHEMISTRY

MEDIZINISCHE KOLLOIDLEHRE. *Lieferungen 12, 13 und 14 (Schlusslieferung).*

Edited by L. Lichtwitz, Raph. Ed. Liesegang and Karl Spiro. Theodor Steinkopff, Dresden. 5 marks each. 10⅜ x 7⅜; pp. 849–1084; 1934 (paper).

These three numbers complete an excellent work on colloid chemistry and its application to medicine. The earlier numbers have been noticed in these columns at various times. The subjects treated in the present *Lieferungen* are: Relations between pharmacology and colloid theory, by E. Starkenstein; Radiation therapy, by R. E. Liesegang; Bandage materials, by Hans Moser; The Wasserman and gold reactions from the standpoint of colloid chemistry, by Carl Lange; Tests for kidney functioning, by F. Hermann; Methods of histological technique from the standpoint of colloid chemistry, by K. Zeiger; Internal medicine, by L. Lichtwitz; Colloid chemistry and surgery, by C. Häbler; and Gynecology and obstetrics, by J. Voigt. The last number is equipped with author and subject indices for the complete series.

LANE MEDICAL LECTURES: BIOCHEMICAL STUDIES OF NUTRITIONAL PROBLEMS.

By J. C. Drummond. Stanford University Press, Stanford University. $1.00 (paper) $1.50 (cloth). 10 x 6¾; 106; 1934.

A series of lectures given at Stanford University. The author is Professor of Biochemistry and Dean of the Faculty of Medical Science at the University of London, and an outstanding figure in the study of nutrition. The titles of the five lectures are as follows: The character of modern problems of nutrition, the "protein factor" in nutrition, the nutritional value of fats, the fat-soluble vitamins in nutrition, the water-soluble vitamins in nutrition. Tables and figures are included in the text, references to literature are given, and at the end of the publication is an index.

BIOCHIMIE DE LA CONTRACTION MUSCULAIRE. *Actualités Scientifiques et Industrielles 113. Exposés de Physiologie, II.*

By Théophile Cahn and Jacques Houget. Hermann et Cie, Paris. 12 francs. 10 x 6½; 43; 1934 (paper).

The chemical changes that take place on contraction of striated muscles as observed from analysis of muscle extracts, experiments on muscles, isolated and *in vivo*, etc. are here briefly but adequately summarized. Due credit is given to the several investigators but exact references and bibliography have been omitted.

HORMONES ET VITAMINES. *Un aspect du problème des quantités infinitésimales en biologie. Actualités Scientifiques et Industrielles, 136. Exposés de Biologie Générale en Rapport avec la Cytologie, II.*

By Z. M. Bacq. Hermann et Cie, Paris. 8 francs. 10 x 6½; 29; 1934 (paper).

A review of the chemical properties and physiologic actions of those hormones and vitamins which have been more extensively and securely identified. There is an excellent bibliography.

SEX

SEX AND CULTURE

By J. D. Unwin. Oxford University Press, London. $12.00. 9¾ x 6⅛; xxiii +676; 1934.

Moved by a desire to test the applicability of the psychological theory of sublimation to social groups, Dr. Unwin examines in a scholarly manner, in great detail and with an astounding wealth of evidence the sexual taboos and religious culture of some 80 uncivilized peoples. Correlation between the number and severity of taboos and the religious culture leads him to conclude (p. 300):

1. All the zoistic societies permitted pre-nuptial sexual freedom; conversely, all the societies which permitted that freedom were in the zoistic condition.
2. All the manistic societies had adopted such regulations as compelled an irregular or occasional continence; conversely, all the societies which had adopted such regulations were in the manistic condition.
3. All the deistic societies insisted on pre-nuptial chastity; conversely, all the societies which insisted on pre-nuptial chastity were in the deistic condition.

The author denies that this simply means that greater formal restrictions accompany higher cultural states but insists instead (p. 302) "If, therefore, there is any causal relationship between a reduction of sexual opportunity and cultural condition, the continence must have caused the thought which produced the change in ideas, and so the cultural change. The contrary cannot have been the case." He adds (p. 326) that the full effect of extension or limitation of continence is reached in a hundred years.

The author goes on to argue that his conclusions and derived laws are verified in the rise and fall of the Sumerians, the Babylonians, Greeks, Romans, Anglo-Saxons, and English, the history of which peoples he sketches very briefly. Needless to say it appears true in each instance. And the author, with evident faith in the power of mind over matter ventures to summarize and advise (p. 432):

> If . . . a vigorous society wishes to display its productive energy for a long time, and even forever, it must re-create itself, I think, first, by placing the sexes on a level of complete legal equality, and then by altering its economic and social organization in such a way as to render it both possible and tolerable for sexual opportunity to remain at a minimum for an extended period, and even forever. In such a case the face of the society would be set in the Direction of the Cultural Process; its inherited tradition would be continually enriched; it would achieve a higher culture than has yet been attained; by the action of human entropy its tradition would be augmented and refined in a manner which surpasses our present understanding.

THREE ESSAYS ON SEX AND MARRIAGE. *By Edward Westermarck. The Macmillan Co., New York.* $6.00. 8½ x 5½; ix + 353; 1934.

In the first of these essays the distinguished author of *The History of Human Marriage* criticizes the work of Freud and his followers on the Oedipus complex. The psychoanalytic method, he concludes, is liable to lead to errors, first because memory, as has been shown by Stern and others, is far from infallible, and second because the leading questions of the analyst are likely to distort the facts still farther. Freud interprets such customs as totemism, exogamy and the killing of the divine king as reminiscences of the primeval crime by which the sons killed and ate their father in revenge for his preventing them from enjoying the women of the family and then, filled with remorse, passed a self-denying ordinance renouncing intercourse with their mothers and sisters. These customs, however, Westermarck concludes, are susceptible of more satisfactory interpretations.

The second essay deals with the recent theories of exogamy of Briffault, Mrs. Seligman, Malinowski and Lord Raglan. Westermarck himself derives the incest prohibition from the "absence of erotic feelings between persons living very closely together from childhood."

The third essay is a rejoinder to Briffault's *The Mothers*. Briffault, as Havelock Ellis remarks, "might seem to belong to that class of controversialists who hold that we should reply not to what our adversary actually said, but to what he ought to have said if we are to triumph over him." Much of the essay is therefore devoted to a correction of Briffault's misquotations of Westermarck and of the authorities whom he had cited. The remainder deals with fresh material which has appeared since the latest edition of *The History of Human Marriage*. This confirms Westermarck in his conclusions that more or less permanent sexual partnerships are found among various species of mammals, including the anthropoid apes, that the unit of organization of primitive man was probably the family consisting of father, mother and children, rather than the promiscuous herd, as Briffault contends, that premarital intercourse is condemned in about half of the uncivilized peoples about whom there is information, that the evolution of marriage is from monogamy to polygamy and back again to monogamy and that polyandry, the lending of wives to guests and other customs which Brif-

fault regards as derived from the primitive group marriage which he postulates cannot be so interpreted. When one considers the wide variation in the customs of different peoples and the variety of unknown factors that may have influenced their evolution it seems to at least one reader that any conclusions as to the origin of the family or of exogamy can at best be no more than probable.

HUMAN STERILITY. *Causation, Diagnosis, and Treatment. A Practical Manual of Clinical Procedure.*

By Samuel R. Meaker. The Williams & Wilkins Co., Baltimore. $4.00. 9 x 6; xv + 276; 1934.

The author points out that the "time has not yet come for an exhaustive treatise on human sterility, since many details of the problem remain imperfectly understood. . . ." Nevertheless, within the last twenty years, significant progress has been made, particularly in the clinical management of involuntary sterility. Doctor Meaker is a pioneer in this field and his book with its clear discussion of the many phases of the diagnosis and treatment of sterility and its extensive clinical records will be of valuable assistance to those of the medical profession who have such cases to deal with. It also lays the foundation for future work along this line. The three main sections of the volume are: Causation of human sterility, diagnostic study of the sterile mating, and treatment of sterility. Figures and tables occur in the text. There is a bibliography of 66 titles and an index. A brief foreword is contributed by Doctors G. W. Kosmak and R. L. Dickinson.

CONCEPTION PERIOD OF WOMEN.

By Kyusaku Ogino. English translation by Yonez Miyagawa. Medical Arts Publishing Co., Harrisburg, Pa. $2.00. 7⅝ x 5; 95; 1934.

This little volume on the so-called "safe period" is one of the numerous tracts published recently upon the subject. It cannot be classed as propaganda, though it can be used as a strong argument by those who advocate the "natural" method of birth control. The figures given by Ogino happen to agree with those of Knaus; hence the O.K. (Ogino Knaus) theory. Knaus claims that ovulation occurs 14 days, and Ogino 11 days, before the onset of the succeeding menstrual flow. Ogino arrived at his conclusion through inspection of ovaries at laparotomy, by no means a new method; and he records the experiences of his patients with the safe period. When his method is correctly used the results are alleged to be 100 percent successful, though whether a patient's statements can be classed as complete evidence is open to question.

THE POWER TO LOVE. *A Psychic and Physiologic Study of Regeneration.*

By Edwin W. Hirsch. Alfred A. Knopf, New York. $4.00. 8½ x 5¾; xxi + 363 + ix; 1934.

Notwithstanding its title this book is a good popular presentation of the causes and therapy of male sexual incompetency. With some foundation, the author expresses the opinion that not enough attention has been given to the psychogenic factors and this is the reason for the doubtful results derived from medical and surgical intervention. He therefore gives in minute details the technique of coition which he considers most efficacious in attempting to overcome psychic impotence. A book that can well be recommended to men young and inexperienced in sexual matters.

GESCHLECHTSENTSTEHUNG UND WILLKÜRLICHE GESCHLECHTSBESTIMMUNG.

By E. Kramer. Deutsches Verlagshaus Bong und Co., Berlin and Leipzig. 3.50 marks. 9½ x 6⅝; 40; 1934 (paper).

After disposing of all previous beliefs about the controlling of sex as erroneous, the author gives a detailed discussion of the chromosome theory of sex determination upon which his particular pet theory is based. Since there is a deviation from the expected 50:50 sex-ratio in all verte-

brates studied, the author says there must be a modifying factor and believes that it can be traced to the differential pH toleration of the x and y sperms. Alkalization of the vaginal tract in 74 normal women resulted in all cases in male births. Attempts to produce females have not been successful.

THE NEW ART OF LOVE. *A Practical Guide for the Married and Those About to Marry.*

By George R. Scott. John Bale, Sons and Danielsson, London. 3s. 6d. net. $7\frac{1}{4}$ x $4\frac{3}{4}$; 117; 1934.

The title is somewhat misleading, as nothing new or original is said about the art of love. But the discussion of the subject is sound, scientific, and free from floweriness or sentimentality. Concerning any disputed point the author cites references, and endeavors to give in every case the most up-to-date information. There is an index.

BIOMETRY

PROFILO DI UNA STATISTICA BIOLOGICA.

By Alfredo Niceforo. Difesa Sociale, Rome. $8\frac{1}{4}$ x $6\frac{1}{8}$; 316; 1933 (paper).

In this volume which appeared serially in *Difesa Sociale*, 1932, 1933, and 1934, Professor Niceforo continues to develop and extend his views on the application of statistical method to different biological problems. Acutely critical, he surveys and reports his own and the investigations of many others as illustrations of the value of statistical treatment which shorn of much of its forbidding mathematical form becomes an elegant means of analysis. With emphasis on the diverse technical approach to the various problems the author considers at length applications to medicine, botany, zoology, anthropology, psychology, genetics, biosociology, and concludes with an excellent exposition of elementary statistical method.

Professor Niceforo's style of writing and profound culture render this book thought provoking both for statistician and layman. For the former because it presents instances of unusual applications, for the latter because it expresses with unusual clarity the object of statistics.

KÖRPERFORM UND SPORTLICHE LEISTUNG JUGENDLICHER KÖRPERMASSE, *Sportliche Leistungen und deren korrelative Abhängigkeit bei 3319 Schülern Münchener höherer Lehranstalten.*

By Emil Breitinger. Emil Breitinger, Linprunstrasse 65, München. RM. 3. $9\frac{7}{8}$ x $6\frac{3}{8}$; 110; 1933 (paper).

Measurements obtained in 1930–31 from approximately 3000 school boys 10 to 20 years of age furnish data for the calculation of means, variability constants, and intercorrelations of anthropometric characteristics (height, weight, height-weight index; trunk, leg and arm lengths; shoulder and pelvic breadths; and chest circumference) and tests of athletic ability (60 meter sprint, standing and running jumps and throwing ability). Attention is directed primarily to the correlations of body form and athletic ability, which, generally, are low except during the adolescent period. The book is a valuable source of data. There is an extensive bibliography.

SANKHYĀ. *The Indian Journal of Statistics. Vol. 1, Part 1.*

Edited by P. C. Mahalanobis. Art Press, Calcutta. 9 shillings net. $11\frac{1}{4}$ x $8\frac{1}{4}$; 154; 1933 (paper).

The title of this journal, published under the auspices of the recently founded Indian Statistical Institute, is a Sanskrit word meaning "determinate knowledge." The editor contributes three papers to the first number: The reliability of a group-test of intelligence in Bengali; Revision of Risley's anthropometric data relating to tribes and castes of Bengal; Tables for the application of L-tests. Other papers deal with Indian prices during the depression, Galton's work on the evidential value of finger prints, and maternity statistics from Mysore.

THE METHODS OF STATISTICS. *An Introduction Mainly for Workers in the Biological Sciences.*

By L. H. C. Tippett. Williams and Norgate, London. 15 shillings net. 8⅝ x 5½; 222; 1931.

This book presents both the classical biometric methods developed by Karl Pearson and his school and the newer methods, centering about the analysis of variance, due largely to R. A. Fisher. Mathematical proofs are given where they are easy, but when they are not the results only are stated. A bibliography of three pages and an index are provided.

TABLES OF THE HIGHER MATHEMATICAL FUNCTIONS. *Volume I.*

Computed and Compiled under the Direction of Harold T. Davis, with the co-operation of Muriel E. Adams, Catherine Bennett, James A. Cooley, Frank K. Edmondson, Edward E. Edwards, Edwin L. Godfrey, H. E. H. Greenleaf, Mabel E. Inco, Lucy C. Kantz, William J. Kirkham, Voris V. Latshaw, Anna M. Lescisin, Lloyd G. Mitton, Edward B. Morris, Paul W. Overman, Irene Price, Marion B. Shelly, Dorothy J. Stephan, John R. Wetnight, Kathryn E. Withers. The Principia Press, Bloomington, Indiana. $6.50. 9¾ x 6¾; xiii + 377; 1933.

This excellent book contains a short history of mathematical tables with reproductions of pages from the 1538 edition of Ptolemy's *Almagest* and the first edition of Napier's *Descriptio*, a bibliography, interpolation formulae with auxiliary tables, and discussion and tables of the gamma and psi functions. Name and subject indexes are provided.

PSYCHOLOGY AND BEHAVIOR

A HANDBOOK OF GENERAL EXPERIMENTAL PSYCHOLOGY.

Edited by Carl Murchison. Clark University Press, Worcester. $6.00. 9 x 5⅞; xii + 1125; 1934.

This is the second volume of what may be called the revised edition of *The Foundations of Experimental Psychology*. With but few exceptions all the chapters have been augmented by the results of the most recent observations. The book is divided into two parts. The first on Adjustive Processes contains articles by W. J. Crozier, T. H. Morgan, A. Forbes, J. G. Dusser de Barenne, W. B. Cannon, P. Bard, C. Landis, C. P. Stone, C. L. Hull, K. S. Lashley, W. S. Hunter and E. S. Robinson. The second part treats of Receptive Processes with papers by L. T. Troland, S. Hecht, C. H. Graham, H. Banister, H. Hartridge, H. Davis, W. J. Crozier and J. P. Nafe. Aside from the eminence of the authors, it can be said that most of the articles are well written and comprehensive from the standpoint of literature and from that of description and interpretation of observations. A useful reference book.

COMPARATIVE PSYCHOLOGY.

By Edward L. Thorndike, R. H. Waters, Calvin P. Stone, F. A. Moss, Donald M. Purdy, Paul E. Fields, Shepherd I. Franz, Howard S. Liddell, W. T. Heron, Edward C. Tolman, Robert C. Tryon, Otto L. Tinklepaugh. Edited by F. A. Moss. Prentice-Hall, New York. $3.50. 8 x 5½; xiii + 529; 1934.

This book is a coöperative one which was planned at the Cornell meeting of the American Psychological Association. Each contributor develops his assigned topic as he sees fit, taking all responsibility for it.

Thorndike's introductory chapter on "Why study animal psychology?" is all too short. The second chapter on historical background is also concise but interesting and readable. The rest of the book is technical. In the chapter on individual differences the statements in regard to inbreeding of animal stocks seem curious to a biologist. That inbreeding may differ in intensity or amount is apparently not considered, but according to this author "inbred stock" should not be used to study individual differences because the individual animals will be too much alike!

DEVELOPMENTAL PSYCHOLOGY. *An Introduction to the Study of Human Behavior.*

By Florence L. Goodenough. D. Appleton-Century Co., New York. $3.00. 7⅞ x 5¼; xvii + 619; 1934.

This excellent textbook deals with the development of behavior from the prenatal period to old age. Among the topics considered are the hereditary background, the prenatal growth of the nervous system, the sense organs, emotional and social behavior in the various periods of growth, intelligence tests, educational and vocational guidance, the maturation and decline of abilities, and mental disease. A bibliography in the form of footnotes and author and subject indexes are given.

SÉMIOLOGIE DU SOMMEIL: *Essai de Neurologie Expliquée.*

By Auguste Tournay. G. Doin et Cie, Paris. 30 francs. 9⅝ x 6¼; 131; 1934 (paper).

The chief merit of this book is that it brings together neurological approaches to the explanation of normal sleep and its symptoms as differentiated from similar states. The experiments of the author, principally on the tendinous and cutaneous reflex actions, some of which become pathological during sleep, are incorporated. He, however, treats them in as critical a manner as the work of others, and no claim is made of a complete solution of the problem. There is a lengthy bibliography, and indices of authors and subjects.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

MIND AND NATURE.

By Hermann Weyl. University of Pennsylvania Press, Philadelphia. $1.50. 8 x 5½; vii + 100; 1934.

These lectures, delivered on the William J. Cooper Foundation at Swarthmore College, deal with some of the philosophical implications of modern physics. As early as Galileo it was recognized that colors and sounds, tastes and odors, were sensations, not properties of objects existing independently of the perceiver, and these secondary qualities were contrasted with primary qualities such as extension and motion which were supposed to exist in the objects themselves. Modern developments in physics have shown that this distinction is not tenable, that space and time are different for different observers. Physics "constructs an objective world in mathematical symbols, but afterwards, to establish the connection with experience, it has to indicate by what procedure the quantities are found which are decisive for immediate perception—decisive in such a way, that equal values of these quantities indicate equal perceptions. In doing that it must of course include the observer as a physical being and his condition in the objective world."